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THE UNIVERSITY OF ALBERTA

THE DEVELOPMENT OF AUTUMN COLORATION IN EUONYMUS ALATA SIEB. 'COMPACTA' IN ALBERTA

by

© Christy Joyce Campbell

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE DEGREE

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FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "The Development of Autumn Coloration in Euonymus alata Sieb. 'Compacta' in Alberta, submitted by Christy Joyce Campbell in partial fulfilment of the requirements for the degree of Master of Science.

Hugh Knowles
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Date March 13, 1979

ABSTRACT

The autumn color of *Euonymus alata* Sieb.'Compacta' growing in North Central Alberta has been observed to be much less brilliant than that of plants growing in Southern Ontario. The response of plants growing under Edmonton (Western) conditions was compared with that of Southern Ontario (Eastern) grown plants and plants exposed to simulated Eastern environmental conditions. As a result of these comparisons, several factors contributing to the marked differences in the autumn color of this plant were isolated.

Leaves that had been exposed to environmental conditions specific to each region during their formation, differed morphologically, anatomically, and in their senescence response. Those formed under Western conditions were much thicker due to development of two to three additional layers of palisade parenchyma cells. Results indicated that regional differences in mid-summer (June - July) photoperiod contributed to the observed difference in leaf anatomy. When temperatures were held at 20°C/7°C (Western temperatures), leaves formed under an eighteen hour photoperiod (Western photoperiod) were 0.0035 mm thicker than those formed under a sixteen hour photoperiod (Eastern photoperiod). This difference in leaf thickness was statistically significant. Cooler Western temperatures also contributed to the greater leaf thickness, although the differences were not significant.

It was further noted when senescence responses were observed under one set of controlled environment conditions (15°C/2°C, 13 hour day), that leaves formed under Western conditions contained 0.0192 mg more

total chlorophyll per square centimeter of leaf tissue at the time of abscission, than those formed under Eastern conditions. This difference was found to be due to the longer day under which leaves in the Western treatment were formed.

Regional environmental conditions during leaf senescence were also found to explain the difference in autumn coloration. In both field and controlled environment studies, Western minimum autumnal temperatures were too low to promote chlorophyll degradation. During the period September 17 to November 8, 1976, the mean total chlorophyll content in leaves exposed to Edmonton field temperatures, decreased only 47.4% (from 0.1290 to 0.0679 mg cm^{-2} leaf tissue). However, when these field temperatures were raised a few degrees at night, the mean total chlorophyll content decreased 89.1% (from 0.1290 to 0.0141 mg cm^{-2} leaf tissue).

Autumnal temperatures also influenced leaf abscission. Under both field and controlled environment conditions, leaf abscission occurred more readily in plants exposed to Eastern autumnal temperatures. Anatomical investigation of leaves in the two field treatments, however, did not show observable differences in development of the abscission layer.

Neither field temperature treatment influenced the one other senescence phenomena studied, that of changing α-amino nitrogen content. Concentrations in both treatments increased in a similar manner during the period studied i.e. September 27 to November 8.

Photoperiod and the ratio of far-red:red light during the light period were both found to influence senescence responses under controlled environment conditions. Senescence and leaf abscission were

delayed when exposed to daylengths typical of the late growing season and early autumn in Edmonton. When plants were exposed to a far-red:red light ratio of 1.7, with all other conditions favoring senescence, leaves took eighteen days longer to abscise, contained 0.0056 mg less chlorophyll and 18.5568 mg more anthocyanin (expressed as mg cyanidin-3-rhamnoside glucoside) per square centimeter than leaves exposed to a far-red:red light ratio of less than 0.5.

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INTRODUCTION

The Dwarf Winged Burning Bush (Euonymus alata Sieb. 'Compacta') is a small (1 m) deciduous shrub with the potential for providing a display of brilliant scarlet foliage at the end of the growing season. In Southern Ontario, full autumn coloration by this plant is commonplace, in Alberta, however, it is minimal and rarely fully achieved.

Autumn coloration in Euonymus is determined by the extent to which two integral aspects of leaf senescence occur, namely chlorophyll degradation and anthocyanin accumulation (Goodwin 1976). Most commonly in Alberta, some anthocyanin accumulation takes place but there appears to be little evidence of a concomitant decrease in leaf chlorophyll.

This study was undertaken to determine the environmental factors affecting the senescence responses of this plant. The effects of treatments designed to separate the influences of temperature, photoperiod, and light quality on autumn leaf coloration and abscission were therefore observed.

The environmental factors affecting leaf morphology were also of interest in this study. Knowles (personal communication) had observed marked morphological differences between leaves of plants growing in Edmonton and those growing in the east where full autumn coloration is achieved. The combined effects of temperature and photoperiod were therefore studied to determine whether or not they affected leaf morphology as well and if so, what influence their affects might have on autumn coloration.

LITERATURE REVIEW

1. Environmental Control of Shoot and Leaf Growth in Woody Plants

The growth of shoots and leaves in woody plants reflects an integrated response to a host of climatic, edaphic, and biotic factors. This effect of environment is not only complex because of the large number of factors involved but also because of the significance of each environmental factor on the various stages of growth (Evans 1972).

Environmental differences can cause a plant to vary greatly in growth response. Total seasonal shoot elongation, growth rate, and bud, leaf, and shoot morphology (Kozlowski 1971) may all be affected. Environment affects growth of woody plants by regulating the expansion of leaf and shoot primordia formed the previous year and by affecting the initiation of new primordia to be expanded in the subsequent year (Kramer and Kozlowski 1960). Environment influences leaf morphology specifically, by affecting the number, distribution, and orientation of cell divisions and by affecting the amount and distribution of cell enlargement (Ashby 1948).

This would suggest that the greatest effect of environment is on young growing tissue. When tissue is mature, environmental influence on morphology is usually limited to the thickness and composition of cell walls (Evans 1972).

Variation within a species found growing in different environments may be due to genetic as well as environmental factors. Genetic differences are manifested when environmental pressures are exerted on mixed genotypes in a local population. Characteristics shown by each ecotype are often related to the photoperiodic or thermoperiodic regime to which a race has been adapted (Billings 1957). It is possible, with controlled environment conditions, to separate individuals with genetically determined differences in growth from those where growth response is solely determined by environmental conditions.

A. Effect of Light

Many of the important physiological and biochemical events that take place during shoot and leaf development are regulated by light intensity, duration (photoperiod) and spectral quality eg. (Dale and Murray 1969, Bradbeer and Montes 1976, Voskresenskaya et al 1977).

1. Light Intensity

Latitude, weather and altitude all affect the total amount of short-wave radiation received at the earth's surface (Anderson 1969). The long term average levels of net radiation[1] and total solar radiation[2] received at Edmonton have been compared with those of geographical locations where E. alata Sieb. 'Compacta' is known to achieve full autumn color: Toronto and Ottawa (Fig. 1, Appendix 1, respectively).

In analyzing these data it is important to recognize that the unit of measurement used, the Langley, (equivalent to 1 gram calorie per square centimeter of irradiated surface) is a meterological one

---

[1] Net radiation refers to the net flux of downward and upward total (solar, terrestrial surface and atmospheric) radiation incident on a surface of unit area per unit of time.

[2] Total solar radiation refers to the total energy incident on a surface of unit area per unit of time.

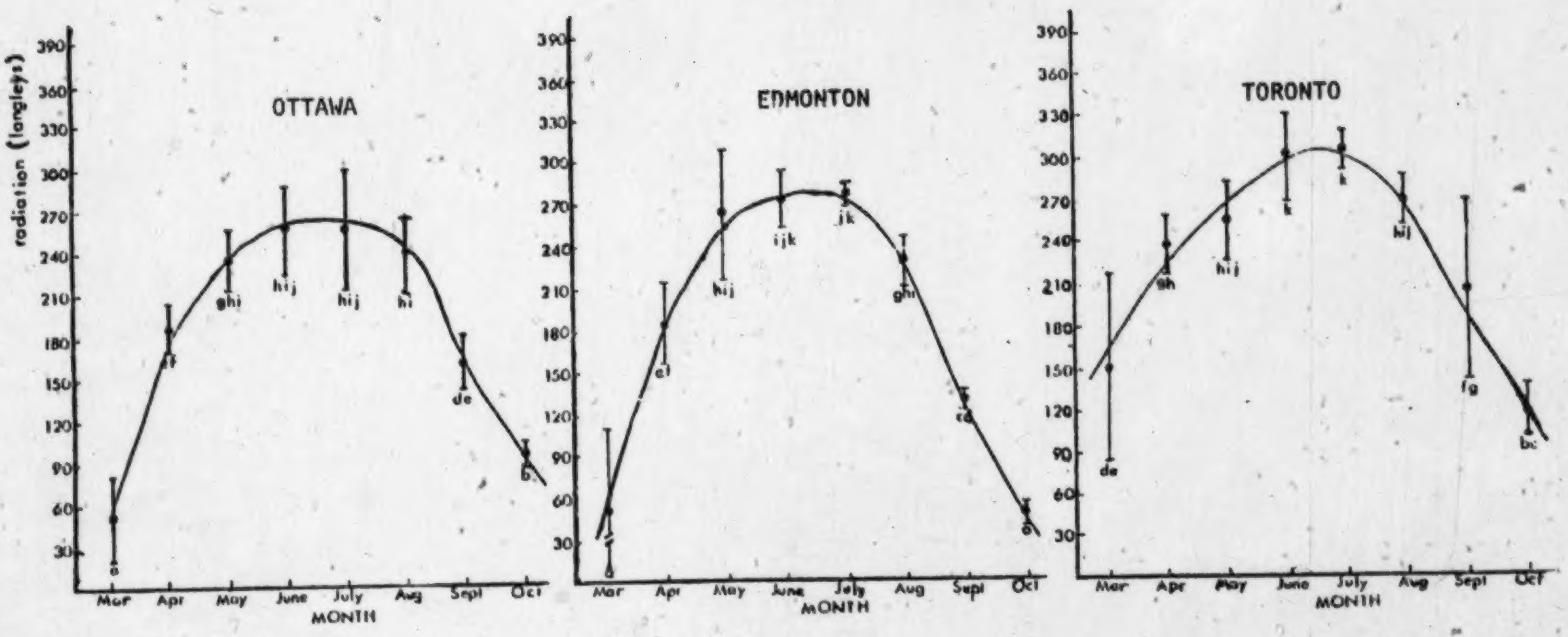

Figure 1. Average monthly net radiation[1] from March to October (1965-74 inclusive) at Ottawa and Toronto, Ontario and Edmonton, Alberta (Environment Canada).

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[1] The length of the line on either side of the mean value indicates the magnitude of its standard deviation. Letters indicate the results of a Duncan's multiple range test conducted on all temperature means for each city, (p=0.05).

representing total solar energy in the range of 300 - 3000 nm. Total solar energy measurements do not relate well, however, to plant growth because such a large portion of the solar radiation measured is beyond the range of photosynthetic and photomorphogenic systems (Downs and Hellmers 1975).

Two statistically significant differences in monthly total solar radiation levels were noted; the level of total solar radiation for May in Edmonton being higher than in both Toronto and Ottawa. A greater number of statistically significant differences were noted in comparing net radiation measurements for identical months between the three cities. Edmonton's March, April and September net radiation measurements were no different than those in Ottawa but were lower than levels encountered in Toronto. Edmonton's October net radiation level was lower than both that of Toronto and Ottawa. No statistically significant differences were found between net radiation levels in the three cities for the months May through August.

Light intensity affects growth of shoots both directly and indirectly (Kramer and Kozlowski 1960). Direct effects of light intensity have been noted on photosynthesis, on stomatal opening and on chlorophyll synthesis, all of which influence plant height, leaf size and leaf and stem structure indirectly.

The effect of light intensity on leaf structure in angiosperms is made apparent by the morphological variation of leaves within the same tree or shrub due to mutual shading and variable exposure to light (Turrell 1936, Wylie 1951, Esau 1965, Bjorkman 1968, Horn 1971 and Wild 1973). A characteristic feature of sun-grown leaves, is the xeromorphic adaptation of an increased proportion of palisade to spongy parenchymatous tissue compared to that in shade-grown leaves (Wylie 1949 and 1951, Talbert and Holch 1957, Kramer and Kozlowski 1960). This effect of increased light intensity also is considered largely accountable for the fact that leaves of alpine plants develop a more massive palisade tissue at higher elevations than at lower elevations.

The increased proportion of palisade to spongy parenchymatous tissue in sun-grown leaves could result from either decreased development of spongy parenchyma cells, increased development of palisade parenchyma cells, or to a combination of both possibilities. According to Haberlandt (1914), increased illumination induces greater development of palisade parenchyma by causing additional layers of palisade cells to be produced. Malinka and Kovalev (1974), however, working with Norway maple, Acer platanoides, found that an increase in light intensity resulted in decreased development of spongy parenchymatous tissue. This is probably a less common occurence than increased development of palisade parenchymatous tissue, as many reports indicate that sun leaves are thicker than shade leaves. As well as being thicker, sun leaves are also smaller, have more strongly developed conducting and mechanical tissues and have thicker walled epidermal cells (Wylie 1949 and 1951, Talbert and Holch 1957, Kramer and Kozlowski 1960). Haberlandt (1914) reports sun leaves as being up to three times as thick as shade leaves.

The chemical composition of sun leaves is also often different from that of shade leaves. Turrell (1939) reported the increase in number of palisade cells in sun leaves may be accompanied by a higher concentration of chlorophyll. On a dry weight basis, Haas et al

(1968) found that sun leaves of Beech, Fagus sylvatica atropunicea had lower concentrations of major and minor elements than shade leaves. Sun leaves also contained less tyrosine, phenylalanine, and methionine and more lysine, histidine, arginine, valine, iso-leucine and proline than shade leaves (Haas 1969).

Leaf adaptations to sun and shade as expected, also influence their photosynthetic capacity over a wide range of light intensities. Sun leaves are photosynthetically less efficient at low light intensities than shade leaves (Kozlowski 1971). However, numerous studies have shown that sun leaves have higher photosynthetic rates at light saturation than shade leaves (El-Sharkawy and Hesketh 1965, Bjorkman 1968, Kozlowski 1971, Grahl and Wild 1973, Duke et al 1976).

It has been suggested that the higher photosynthetic rates of sun leaves at light saturation occur as a result of changes in activity of enzymes involved in photosynthesis due to a different chloroplast structure (Bjorkman 1968, Goodchild et al 1972, Grahl and Wild 1973, Singh et al 1974) and/or from an increase in the concentration of chlorophyll per photosynthetic unit (Bjorkman 1968, Goodchild et al 1972, Pearlstein 1971). Other studies have shown that the gross morphology of a sun leaf also determines the higher photosynthetic rate that it can sustain (Turrell 1936 and 1942, Bjorkman et al 1974, Nobel et al 1975, Gay and Hurd 1976). Gay and Hurd (1976) state this is because stomatal frequency (effective stomatal pore area per unit leaf area) is greater in sun leaves than shade leaves. This increase in stomatal frequency decreases total CO_2 resistance (CO_2 resistance at stomatal openings plus CO_2 resistance at spongy parenchyma cell surface) per unit leaf area and thus allows the observed higher rates of assimilation.

Carrying this further, Bjorkman et al (1975) determined that this decrease in total CO_2 resistance was due to a reduction in the first component of resistance (CO_2 resistance at stomatal openings) caused by an increase in stomatal frequency rather than due to a reduction in the second component of resistance (CO_2 resistance at spongy parenchyma cell surface). The increase in stomatal frequency in sun leaves permits a greater internal cell surface area to be exposed to air than in shade leaves. Nobel et al (1975) drew these conclusions because when illumination, during leaf development of Plectranthus parviflorus, was increased from 900 to 42,000 lux, leaves more than tripled in thickness and the ratio, of internal cell surface area exposed to air to total cell surface area exposed to air, rose from 11 to 50. The net rate of photosynthesis at light saturation also increased by a factor of 4, however, he found that CO_2 resistance, per unit of spongy parenchyma cell surface exposed to air, remained constant for leaves grown under all illuminations.

Although he did not relate it to photosynthetic capacity, Turrell (1936) compared both the internal and total cell surface areas (exposed to air) of leaves of a large number of plants. He also found the ratio of the internal cell surface area to total cell surface area (exposed to air) to be low for shade leaves, intermediate for mesomorphic leaves and high for xeromorphic leaves.

2. Daylength

As the axis of rotation of the earth is not perpendicular to the plane of its orbit around the sun, there is an annual variation in daylength at a given latitude (outside the tropics) with the longest day occuring at summer solstice (Collingbourne 1966). The average daylengths for the months March through November (1965-1974 inclusive) for Edmonton and Toronto are illustrated in Figure 2. Average daylengths for Ottawa were not given as they are almost identical to those of Toronto. Length of day during this period, begins to increase two weeks earlier in Edmonton than in Toronto and, after reaching its maximum at summer solstice, begins to decrease two weeks earlier than in Toronto. However, the longer daylengths, 16 - 18 hours, occur for two weeks longer in Edmonton than in Toronto. The maximum daylength reached in Edmonton is eighteen hours whereas in Toronto it is sixteen hours.

The duration of the daily light period has a major effect on all aspects of woody plant growth (Wareing 1953, Vince-Prue 1975). Many growth phenomena will occur only when daylengths are longer than or shorter than a critical duration. Vince-Prue (1975) points out that under natural conditions some of the daylength effects are not photoperiodic responses per se, but are the result of the influence of the total quantity of light received by the plants on photosynthesis.

The strong influence of photoperiod on plant growth is demonstrated by the occurrence of photoperiodic ecotypes. For example, Demos et al (1975) found, in studies of Eastern Redbud ecotypes, that first stage hardening (photoperiod mediated) was correlated with the latitude of orgin. Pauley and Perry (1954) also observed genetic diversity in shoot growth characteristics of clonal lines of Populus. They stated that when seedlings from northern, long-day, races are planted in southern latitudes with long frost-free seasons, the resulting trees will cease shoot growth early. Seed of ecotypes from

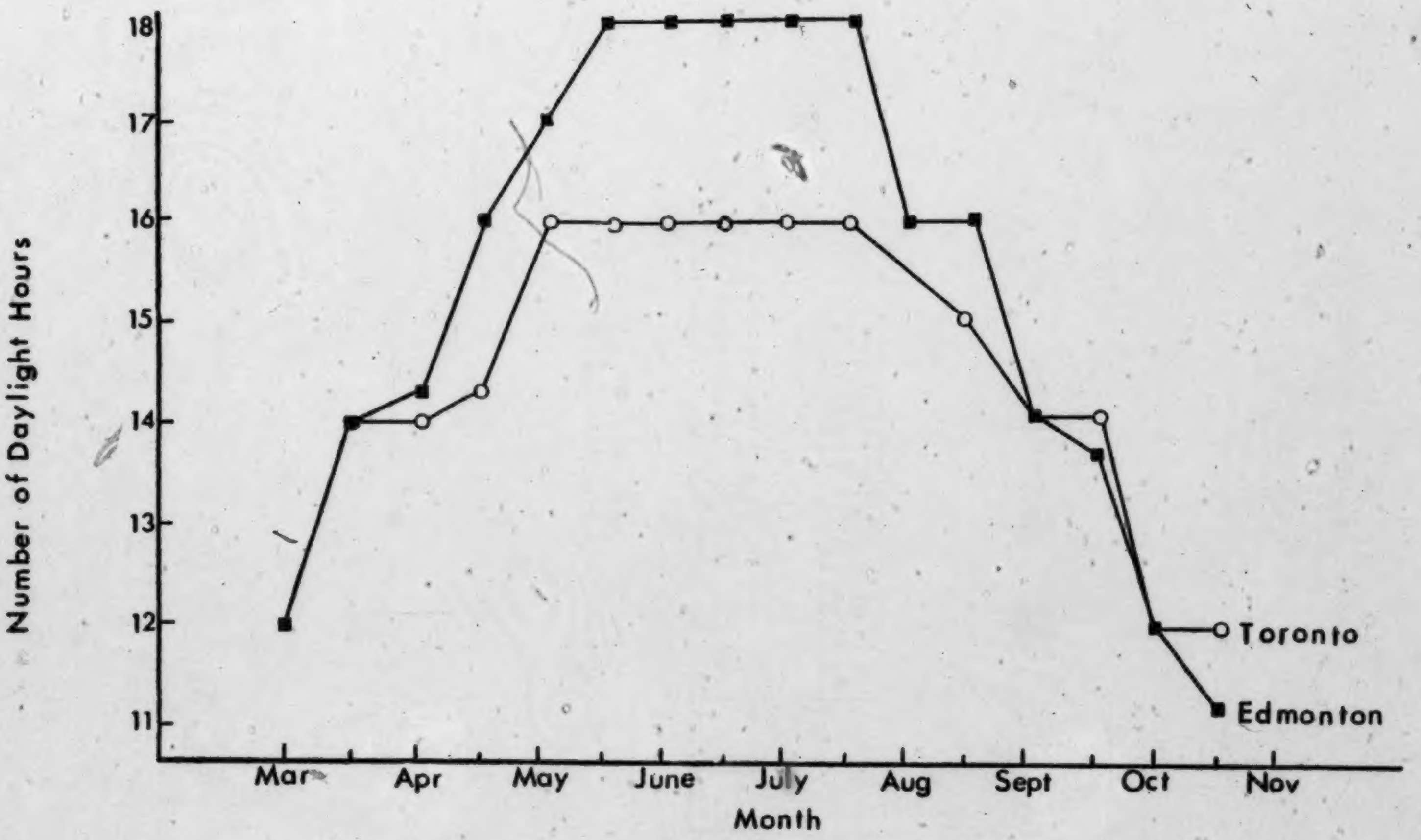

Figure 2. Average daily number of daylight hours[1] for the months March to November in Toronto and Edmonton, 1970 (Environment Canada).

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[1] Daylength for the first 15 days of each month was averaged to compute the average daily number of daylight hours for the first half of each month. Daylength for the days remaining in each month were averaged to compute the average daily number of daylight hours for the last half of each month.

long frost-free seasons planted in habitats with short frost-free periods however, may be damaged by early frost.

Influence of photoperiod, specifically on shoot morphology, has been reported by numerous authors (Harder and von Witsch 1940, Sen Gupta and Payne 1947). In general, it has been noted that long days increase the rate and duration of vegetative elongation of woody plants whereas short days decrease the rate of growth and hasten the onset of terminal bud formation.

Changes in the chemical composition and morphology of leaves have also been observed in response to photoperiod. Tso et al (1970) found that tobacco plants grown under 16 hour days had significantly higher concentrations of total alkaloids and total phenols than those grown under 8 hour days. Kasperbauer et al (1970), also working with tobacco, reported that a long photoperiod resulted in a higher concentration of free sugars and lower concentrations of organic and amino acids than short photoperiods. Daylength has also been reported to affect the composition of essential oils and flavonoids of Chamomile, Anthemis nobilis cultivars (Vince-Prue 1975).

The alteration of leaf morphology by photoperiod can take many forms (Vince-Prue 1975). Cockshell (1966) found that daylength treatments of the China aster, Callistephus chinensis continued to exert an effect through to the last stages of leaf growth when the leaves were three quarters their mature size. An increase in the ratio of leaf length to breadth in response to short days is common (Vince 1955, Thomas 1961). Whatever the photoperiodic class for flowering, leaves of most plants so far examined are also larger under long days than short days (Vince-Prue 1975).

There are conflicting reports as to whether this increase in leaf area in response to long days results in thinner leaves. In long day treatments of China aster, Callistephus chinensis expansion of the leaf surface was accelerated resulting in thinner leaves with an increased specific leaf area[1] (Vince-Prue 1975). Arney (1956) noted in strawberry, however, that the leaves were not thinner under long days and that the increased leaf area was due to an increase in cell number due to prolonged cell division. Margaris and Papadopoulou (1975) have reported that the leaves of Mongolian cherry, Prunus fruticosa formed under long days were thicker and xeromorphic in nature compared to leaves formed under short days. An increase in the proportion of palisade to spongy parenchymatous tissue was observed. Nitsch (1957) noticed, however, that the leaves of Peach, Prunus persica were thicker when grown under long days and that this was due to favored growth of spongy rather than palisade parenchymatous tissue.

3. Light Quality

From a review of current literature, data on the quality of light at various geographical locations is limited at the present time and little extensive work has been done on the effect of altitude, latitude and season on light quality. Robertson (1966), in observing daily changes in light quality, found that natural light in the open from both clear and hazy skies appeared to have a fairly uniform spectral composition for solar elevations greater than 9° of arc above the horizon. Below a solar elevation of 9°, however, the proportion of blue (440 nm) and far-red (740 nm) energy increased with decreasing solar elevations. Below a solar elevation of 4°, near civil twilight where skylight predominates, there was a decrease in the proportion of red (640 nm) light as well as an increase in proportion of blue and far-red light energy. Holmes and McCartney (1975), noting similar changes in proportion of red and far-red light energy with changes in solar elevation, found the rate, magnitude, and duration of these changes to depend on atmospheric conditions. The smallest and most gradual changes were observed under overcast skies.

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[1] specific leaf area = leaf area/total leaf dry weight.

The magnitude of changes in light quality with decreasing solar elevation also varies with latitude and season. Van Zinderen Bakker (1974) measured light quality at twilight, 20 km southeast of Edmonton during 1973 and 1974 (see Table 1). The far-red (750 nm): red (650 nm) light ratio was highest in June and July as is expected at a latitude where there are long periods of summer twilight. With respect to latitude, Robertson (1966) noted that the far-red:red light ratio at a given season and solar elevation below 9° was greater at higher latitudes than at lower latitudes.

Altitude has also been shown to affect light quality received at the earth's surface. For example, Caldwell (1968) investigated the change in long wave ultra-violet radiation (350 - 400 nm) and found that radiant energy in this spectral band was up to fifty per cent higher at 4350 m elevation that at 1670 m.

Many effects of light quality on plant life, both interacting with other photoresponses and occurring independently, have been observed. Perception of light quality by plants involves photoreceptors, of which phytochrome is the best understood (Smith 1976).

Table 1. Far-red (750 nm): Red (650 nm) light ratios measured at twilight 20 km from Edmonton, Alberta throughout 1973-74 (van Zinderen Bakker 1974).

Date	Time (MST) h	Ratio	Comments[1]
May 7 1973	20:00	.95	clear
May 30	20:00	1.00	clear
June 28	21:00	1.06	cloudy
July 21	20:00	1.06	overcast
August 19	20:00	.76	cloudy
September 6	18:00	.93	clear
October 3	18:00	.75	clear
October 18	18:00	1.00	overcast
April 19 1974	17:00	.94	overcast

[1] cloudy - clouds in sky, could lead to readings being made in both full sunlight and shade during the period of measurement.

overcast - no blue sky visible.

For example, it is known that phytochrome exists in two interconvertible forms; phytochrome red (P_r), which absorbs maximally at 660 nm; and phytochrome far-red (P_{fr}); absorbing maximally at 730 nm. P_r is converted to P_{fr} upon irradiation with 600 nm light and P_{fr} is converted to P_r upon irradiation with 730 nm light (Smith 1976).

Photoperiodism is a photoresponse with which light quality has been shown to interact. Funke (1948) and Wassink et al (1957) found that the inclusion of a certain amount of either violet, blue or infrared light in a long day is necessary for long day effects in some plants. They also found that blue light extension of an eight hour period of white light, to provide a long day, was much more effective in producing long day responses than either red or green light.

Wareing (1950) found the cessation of internode elongation and the advent of dormancy to be two photoperiodic phenomena that were controlled separately by light quality. Scotch pine, Pinus sylvestris seedlings were given a short period of natural light in the greenhouse to supply their photosynthetic requirements. They were then illuminated with different qualities of low intensity light to satisfy their requirement of long photoperiods for extension growth. Various internode lengths were obtained with different qualities of supplemental light. However, maintenance of a plant in a non-dormant condition (determined by its ability to break bud under continuous light) was effected equally well by all qualities of supplemental light. Downs and Borthwick (1956) have verified this in similar experiments.

The amount of far-red and red light received by a plant at day's end has also been found to play a part in influencing photoperiodic reactions (Borthwick et al 1952). In experiments with tobacco, Kasperbauer et al (1970) and Tso et al (1970) found distinct morphological and chemical differences between plants given either five minutes of red or far-red radiation at the end of each day. Morphological differences were more pronounced when the red and far-red treatments were given at the end of an eight hour photoperiod than the end of a sixteen hour photoperiod. Downs (1959) noted a greater increase in growth of loblolly pine, Pinus taeda under long days if plants enter the dark period following short irradiation with far-red rather than red light. It is assumed these morphological differences resulted from the effects of the different phytochrome photoequilibria produced in the plants by the treatments provided.

As mentioned earlier, light quality also influences plant growth in ways independent of other photoresponses. Kakhnovich and Grits (1975) found that the content of total labile and firmly bound leaf chlorophylls in chloroplasts isolated from pea, Pisum sativum 'Ramonskii' also depended on spectral composition of light. The labile form was present in greater concentrations under blue light than under red light. This was believed attributable to increased de novo synthesis of chlorophyll. The concentration of the firmly bound form was also greater under blue light than red light. This increased concentration of firmly bound chlorophyll was attributed to a promotion by blue light, of rapid fixing of the labile form of chlorophyll. Downs et al (1958) found that expansion of leaf blades of loblolly pine, Pinus taeda and Western Yellow pine, Pinus ponderosa was least under green light, intermediate under blue light and greatest under white light.

The majority of experiments involving the effect of light quality on tree growth and the role of phytochrome in influencing growth responses have been carried out by exposing etiolated plants to light composed of only a narrow range of wavelengths (Wassink and Stolwijk 1956). This, however, is very different from natural conditions, where visible and invisible radiation consisting of a wide rather than a narrow range of wavelengths, impinge on green leaves.

In assessing the effect of light quality in the natural environment on plant growth, Robertson (1966) has suggested that the long period of twilight rich in blue and far-red energy, occurring at high altitudes such as Edmonton, may affect plant growth. Morgan and Smith (1976) state, however, that growth form is not greatly affected by changes in light quality at sunrise or sunset. They have conducted various experiments that indicate growth form is mainly altered by the quality of light throughout the entire light period. Daubenmire (1959) considered light quality to have a relatively unimportant influence on growth and development under natural conditions as compared to the influences of light intensity and photoperiod. He based this statement on the facts that each physiological process is sensitive to all wavelengths of light and responses to specific wavelengths vary among species. It must be remembered in evaluating this statement, however, that much information on the effects of light quality on plant growth have been gained since 1959.

Although the involvement of phytochrome in determining growth responses of etiolated plants to light of narrow spectral regions has been demonstrated, until relatively recently there has been no direct evidence on the function of phytochrome in the natural environment

(Morgan and Smith 1976). This is because in etiolated plants, phytochrome can be induced to exist in one of its two forms by irradiation with light of the proper wavelength and the effect on growth observed. However, in continuous irradiation with broad-band sources absorbed by both P_r and P_{fr}, a photodynamic equilibrium is achieved characterized by steady state proportions of P_r and P_{fr}. This photoequilibrium is usually denoted by the ratio, P_{fr}; P_{total}. Holmes and Smith (1975) have shown that the ratio, P_{fr}: P_{total} can be quantitatively related to the ratios of quantum flux densities at 660 nm and 730 nm in a wide range of radiation sources.

Morgan and Smith (1976) have provided some evidence for the function of phytochrome photoequilibrum in influencing stem elongation, branching, flowering and leaf pigmentation in the natural environment. For example, using different far-red: red light ratios but equal amounts of photosynthetically active radiation (PAR), to produce different phytochrome photoequilibra, the logarithmic rate constants of stem elongation were found to be linearly related to the phytochrome photoequilibrium. Studies of the spectral energy distribution within forests have led Holmes and Smith (1975) to suggest that, in the detection of shading by other plants, phytochrome may be involved. This suggestion is based on the previously documented observation that leaf canopies transmit green and red light to a lesser extent than blue and far-red light (e.g. Federer and Tanner 1966). The greater depletion of red light in comparison with far-red light when radiation is attenuated by leaves may be expected to decrease the proportion of phytochrome existing as P_{fr} in leaves and thus alter the photoequilibrium. Such a change in phytochrome photoequilibrium would then lead to those differences in plant growth and development characteristic of shady environments.

B. Effect of Temperature

The maximum and minimum temperature norms for the years 1941-1970 (Environment Canada 1971), March through April, in Edmonton, Ottawa and Toronto are shown in Table 2 and again in Figures 3 and 4. Throughout the entire period maximum and minimum temperatures at Edmonton were lower than those at both Toronto and Ottawa. Edmonton's autumn temperatures normally fell below the freezing level one month earlier than in Ottawa and two months earlier than in Toronto. In the spring, minimum temperatures in Edmonton remain below freezing one month later than in both Ottawa and Toronto.

Studies illustrating temperature effects on all aspects of plant growth are documented by Went (1953). It is also well known that temperature is a major factor in limiting plant distribution and in determining the behavior of plants when they are moved to other environments (Kramer 1943, Kaszkurewicz and Fogg 1967, Tranquillini and Unterholzer 1968). Kaszkurewicz and Fogg (1967) compared shoot growth under controlled conditions of two lots of plants each consisting of Cottonwood, Populus deltoides and London Plane, Platanus occidentalis. One lot was adapted to the temperature regime of low altitude, the other to that of high. Shoot growth of plants adapted to the higher altitude was less than that of plants adapted to the lower altitude. This difference in shoot growth was found to be the result of both a delay in bud opening and in an earlier cessation of shoot growth by plants from higher altitudes. Kramer (1957) has shown that when the shoot is actively expanding, growth is affected more by the difference

Table 2: Normal[1] monthly maximum and minimum temperatures for Edmonton, Toronto and Ottawa, March to November.

		MONTH								
	City	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov
Maximum °C	Edmonton	-0.6	9.6	17.0	20.4	23.4	21.7	16.7	11.1	-0.1
	Toronto	4.2	11.9	17.9	24.2	26.8	25.9	21.6	15.3	7.8
	Ottawa	1.3	10.9	18.3	24.0	26.4	25.1	20.1	13.8	5.1
Minimum °C	Edmonton	-10.3	-1.6	4.7	8.8	11.5	10.1	5.0	-0.2	-8.4
	Toronto	-2.9	3.2	8.4	14.1	16.8	16.2	12.3	7.1	1.8
	Ottawa	-7.5	0.3	6.5	12.3	14.7	13.5	9.1	3.6	-2.4

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[1] Normal values are based on the period 1941-1970 (Environment Canada (1971).

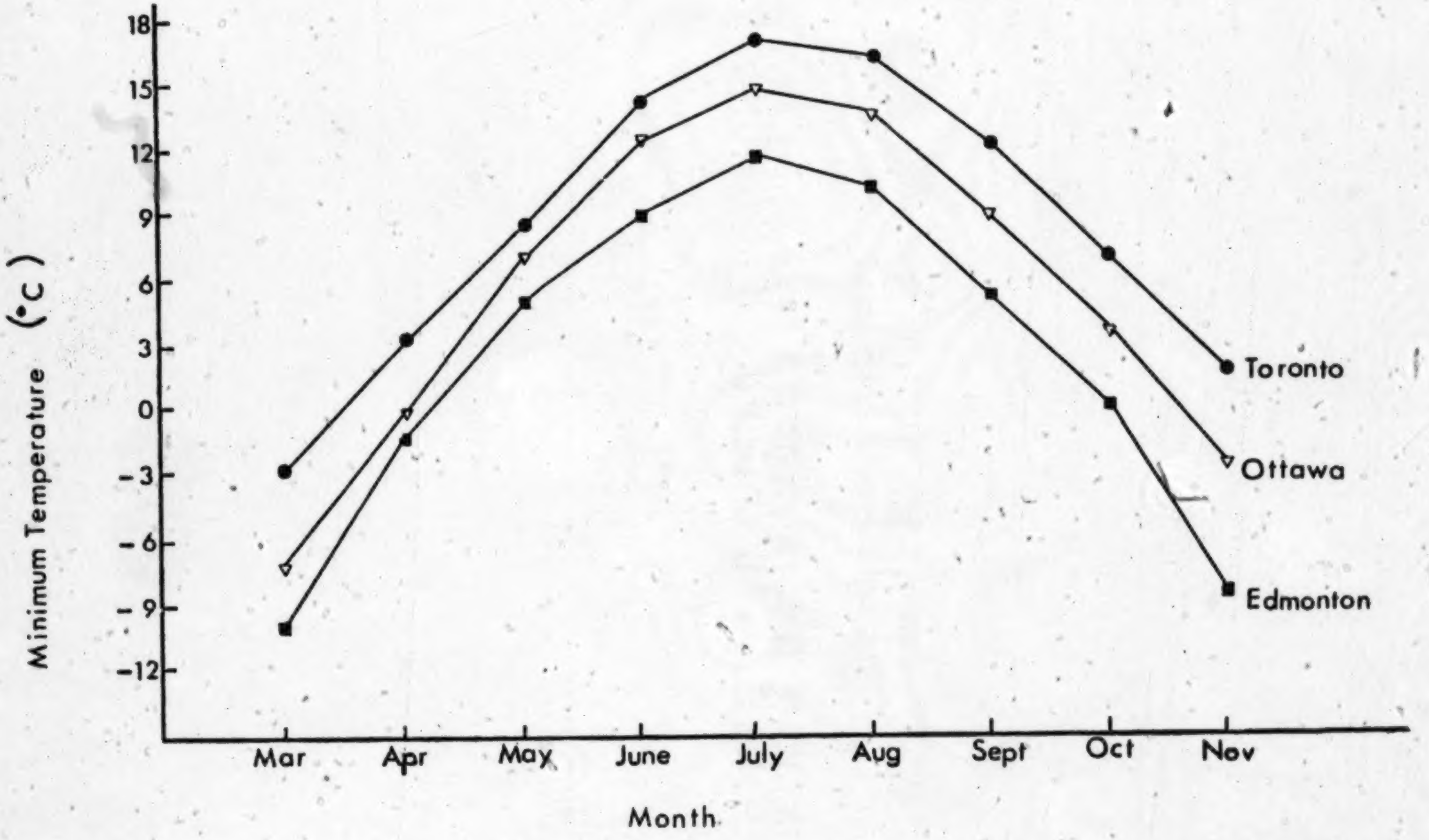

Figure 3. Normal monthly minimum temperatures for the period March to November (1941-1970 inclusive) in Toronto, Ottawa and Edmonton (Environment Canada 1971).

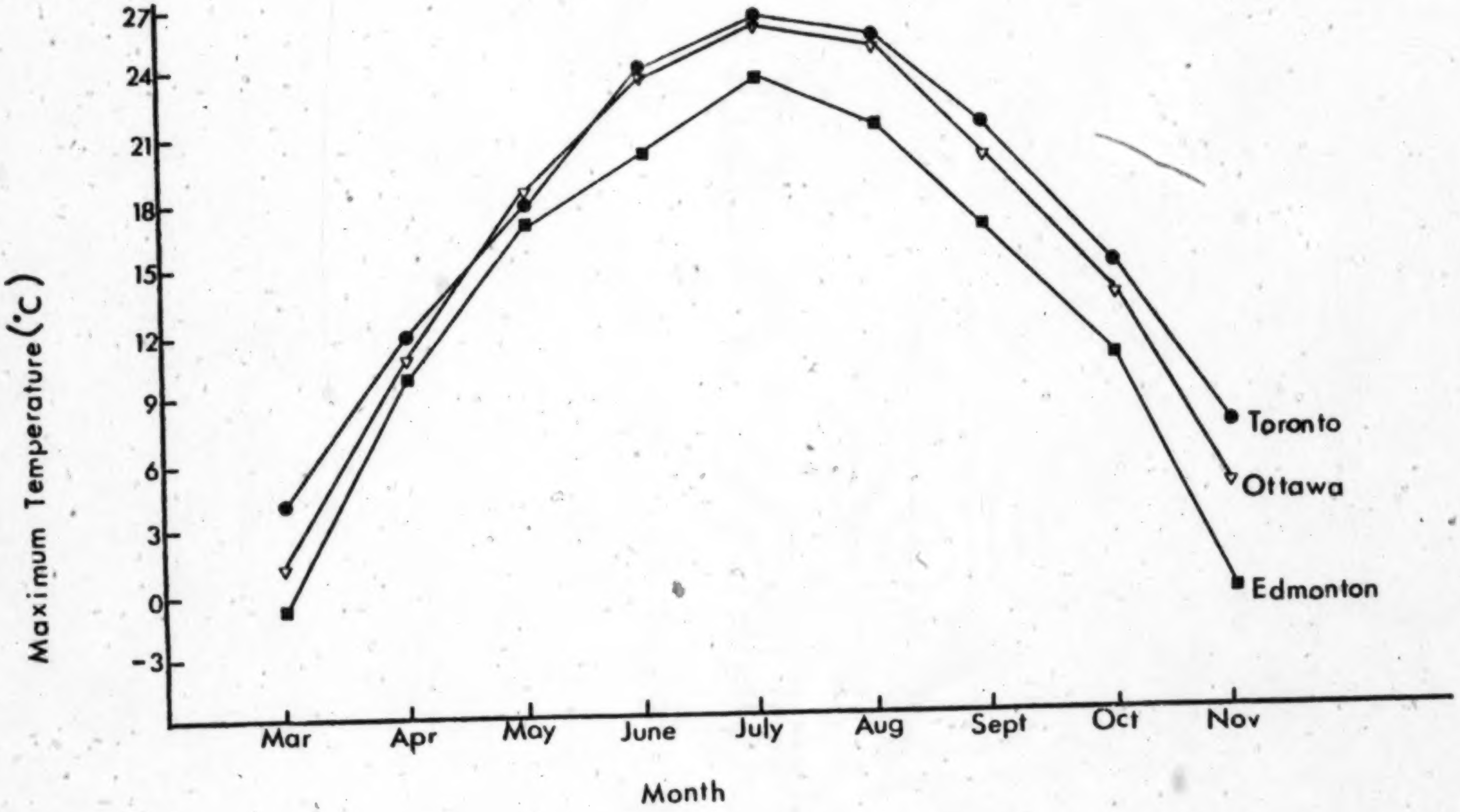

Figure 3. Normal monthly maximum temperatures for the period March to November (1941-1970 inclusive) in Toronto, Ottawa and Edmonton (Environment Canada 1971).

between day and night temperature than by average daily temperature.

Changes in temperature during the growing season, as well as at the time of budbreak, also influence shoot growth (Kramer and Kozlowski 1960). Small daily changes in temperature are not detrimental to plant growth and are associated with variation in shoot growth through their direct effects on photosynthesis, transpiration, hormone synthesis, respiration, chlorophyll synthesis, enzyme activity, cell division and elongation. Large daily changes in temperature to either abnormally high or low levels, on the other hand, can cause damage to growing shoots.

II. Leaf Senescence and Abscission

Leaf abscission is an integral part of leaf senescence. Anatomical changes at the base of the leaf petiole to effect leaf abscission ordinarily occur only when there are evident signs of senescence (dela Fuente and Leopold 1968). It follows that those factors that influence senescence also influence abscission.

A. Biochemical Changes

Many biochemical changes are associated with leaf sensecence: starch hydrolysis, changes in photosynthetic and respiration rates, enzymatic activity, dry weight and concentration of pigments, protein, minerals, RNA and DNA (Addicott 1968, Kozlowski 1971).

Photosynthetic capacity of leaves is maximal near completion of most rapid growth but decreases with further aging until it reaches its minimum rate at leaf abscission (Rhoads and Wedding 1953, Richardson 1957).

As leaves age, respiration per unit dry weight also steadily decreases (Salisbury and Ross 1969, Kozlowski 1971, Osborne 1973). This is largely due to thickening of cell walls (Kramer and Kozlowski 1960). Osborne and Hallaway (1960) noted an exception to this common observation. An increase in respiratory activity in senescing leaf disks of Japanese cherry, Prunus serrulata was observed before the decrease in respiration per unit dry weight. There was an increase in oxygen uptake as soon as the leaves were removed from the tree, with a peak reached in ten days. After this initial rise there was a continuous decrease in respiration which corresponded to a slow decrease in protein content.

Mineral nutrition of plants affects the process of leaf abscission in that when essential nutrients are ample, leaves are retained longer (Addicott and Lynch 1955). During senescence, loss of certain mineral nutrients from the leaf back into twigs and branches and by leaching from senescent cells has been demonstrated (Oland 1963).

1. Nitrogen Compounds

Changes in the nitrogen metabolism of naturally senescing leaves and of leaves induced to senesce by removal from the plant, have been measured. An observation, common to both materials, is the increase in amino acid and amide concentration as senescence progresses (Yemm 1937, 1950). The source of these alcohol soluble materials could be either from synthesizing activity (Chibnall and Wiltshire 1954, Yemm 1956), from protein catabolism (Wood et al 1944, Cruickshank and Wood 1945) or from a combination of both.

There is considerable evidence that the increase in amino acids and amides during abscission arise from protein catabolism. Plaisted (1958a) has shown that the protein content in leaf tissue of Norway Maple, *Acer platanoides* declines sharply approximately 50 days before natural abscission. Similar results were noted by Sampson and Samisch (1935) in Oak, by Olsen (1948) in Beech, and by Osborne (1962) in Cocklebur. Osborne (1962) noted that the quantity of soluble nitrogen compounds tended to parallel total protein content in leaves of Cocklebur but increased just prior to abscission. Lee and Tukey (1971) reported a steady decrease in the ratio of protein nitrogen to soluble nitrogen in Burning Bush, *Euonymus alata* during the month preceding abscission. Changes in the absolute quantities of protein and soluble nitrogen however, were not reported. Plaisted (1958a) showed that the decline in soluble nitrogen compounds in leaves of Norway Maple, *Acer platanoides* stopped about thirty days before abscission and then showed a slight increase. This was likely associated with proteolysis of chloroplast protein. It was suggested that a block in the translocation system would allow a buildup of this soluble product to the levels observed. Plaisted cites Lee (1911) who noticed accumulation of tyloses in the vessels of Sycamore Maple, *Acer pseudoplatanus* just before abscission. Plaisted states that although conventional theory associates upward translocation with the vessels, a partial block of a similar nature may exist in the phloem which would decrease translocation out of the leaf. In working with cucumber cotyledons, Lewington et al (1967) state that since the shape of the protein and chlorophyll degradation curves are similar and since a large proportion of leaf protein is in the chloroplasts, it is very likely that the observed decline in both protein and chlorophyll is the result of chloroplast breakdown.

Decreased levels of DNA and RNA have also been observed in aging tissue (Plaisted 1958a, Leopold 1961, Osborne 1962 and 1965, Lewington et al 1967). Kozlowski (1971) states that the decreased ability of cells to synthesize DNA, RNA and thus protein, appears to be a crucial malfunction which promotes senescence.

2. Chlorophyll

Aging leaves usually lose their green color during senescence and appear either yellow, red or brown before abscission (Wolf 1956). As a result of chlorophyll degradation, leaves may appear yellow due to unmasking of the more stable carotenoid pigments or brown due to the unmasking of tannins. Red leaf colour, on the other hand, is determined by the extent to which two senescent processes occur: anthocyanin synthesis (by plants with the genetic capability) and chlorophyll degradation. Thomas and Stoddard (1975) suggest, however, that chlorophyll breakdown is not necessarily an inevitable part of aging. They base this suggestion on the discovery of a mutant genotype of meadow fescue, Festuca pratensis Huds. whose chlorophyll does not breakdown during senescence when other senescent processes are proceeding normally.

The rate and extent of chlorophyll degradation before leaf abscission varies greatly among species. For example, Kozlowski (1971) reports rapid breakdown of chlorophyll (35 days) in Magnolia, Magnolia kobus borealis and disintegration occuring over 60 days in Mulberry, Morus alba. Only 40% of the chlorophyll in lilac was degraded before leaf abscission. However, much higher levels of chlorophyll degradation have been observed in other tree species (Seybold 1943, Jeffrey and Griffith 1947). In the species studied by Wolf (1956), chlorophyll degradation during senescence averaged 84.9%. In most species studied, chlorophyll a was destroyed more rapidly than chlorophyll b. Goodwin (1976) states this phenomema is not due to physiological selection but to a difference in chemical reactivity.

It should be noted that under water or temperature stress, leaves may be shed green, and that some metabolic processes such as protein synthesis (Gates and Bonner 1959, Mothes 1964, Genkel et al 1967) and photosynthesis (Genkel et al 1967) are reduced to levels found in non-green senescent leaves.

The ultimate fate of chlorophyll during senescence remains unsolved, although there appears to be a rapid cleavage of the chlorophyll molecule into small fragments which are subsequently oxidized (Goodwin 1976). The enzyme, chlorophyllase (chlorophyll chlorophyllidohydrolase, EC 3.1.1.14) has been isolated by Willstater and Stoll (1910), however, its physiological role has not yet been determined (McFeeters et al 1971, Goodwin 1976).

3. Anthocyanin

Red autumnal leaf color is partially provided by the synthesis of anthocyanins, most often by the simplest anthocyanin, cyanidin-3-glucoside (Hayashi and Abe 1955). Anthocyanins are water soluble pigments formed by reactions between various sugars and anthocyanidins, the aglycosidic portion of the anthocyanin molecule. Anthocyanins occur not only as monomers but also as parts of much larger complexes. These exist in loose association or in chemical combination with other components (Barz and Hösel 1975). Anthocyanins in leaves are usually restricted to either epidermal or spongy parenchyma cells (McClure 1975).

Until recently, flavonoids (the name given to the class of chemical compounds of which anthocyanins are a part) have been considered inactive end products of secondary plant metabolism. However, evidence for their catabolism has recently been demonstrated. The level of anthocyanins in senescing tissue can now be considered a reflection of the efficiency of primary metabolism tempered by turnover and degradation of synthesized secondary compounds (McClure 1975).(See Figure 5).

The mediation of primary metabolism in anthocyanin synthesis is well substantiated. For example, an increase in the carbohydrate status of tissue whether by feeding simple sugars or by natural means, frequently results in stimulation of anthocyanin formation by those species with the genetic potential (Eddy and Mapson 1951, Thimann et al 1951, Eberhardt 1954). An inverse relationship between anthocyanin formation and protein synthesis has also been shown (Faust 1965, Harborne et al 1975). The link between protein synthesis and anthocyanin formation and the relationship between anthocyanins and other flavonoid compounds is illustrated in Figure 6.

B. Anatomical Changes

The abscission zone begins to form, in most woody plants, relatively early in the growing season (Facey 1950, Webster 1968, Moline and Bostrak 1972). Days, or even weeks prior to the shedding of the leaf, abscission tissue termed the separation layer, develops in

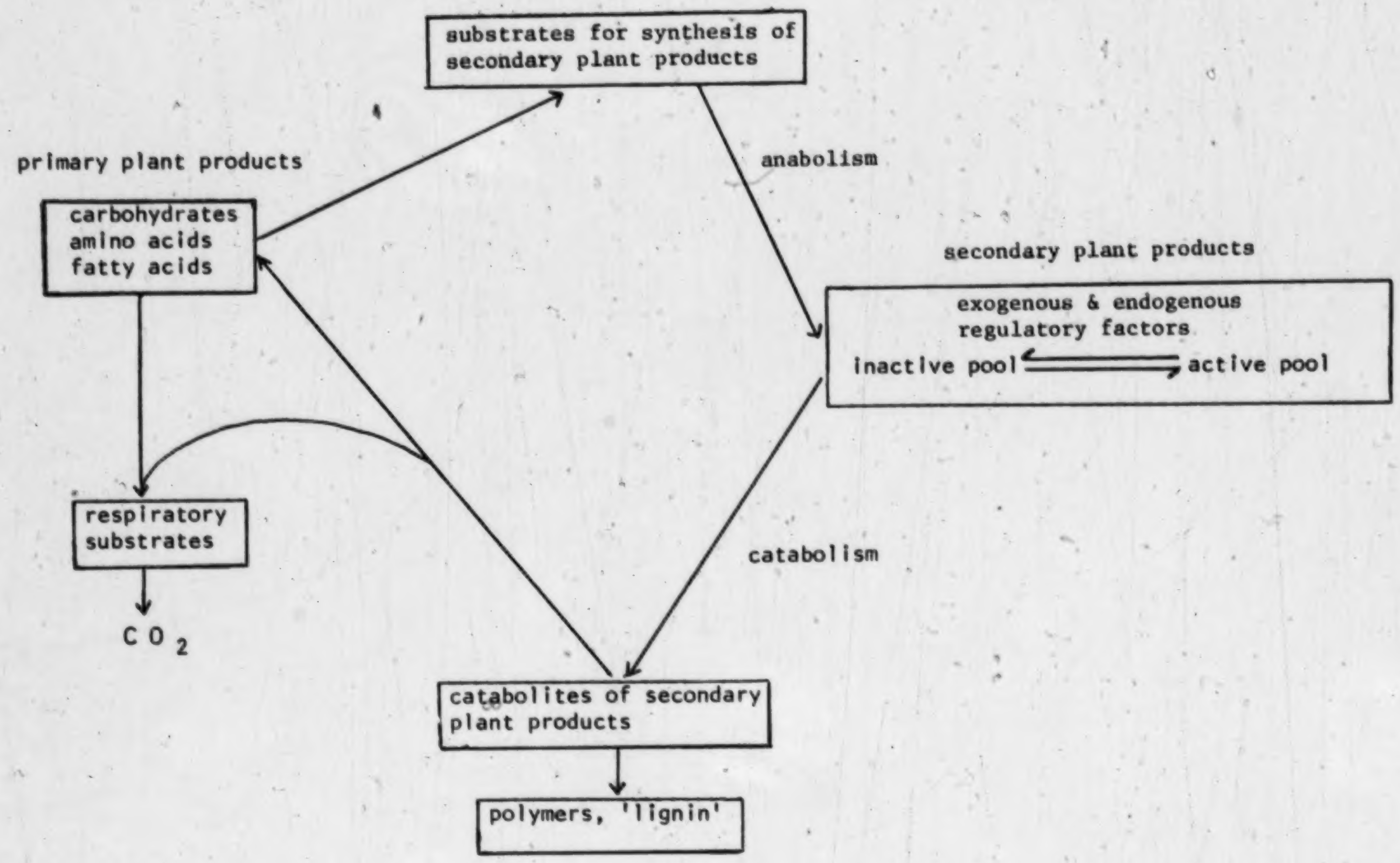
substrates for synthesis of secondary plant products
primary plant products
carbohydrates
amino acids
fatty acids
anabolism
secondary plant products
exogenous & endogenous regulatory factors
inactive pool
active pool
respiratory substrates
C O 2
catabolism
catabolites of secondary plant products
polymers, 'lignin'

Figure 5. Relationship between primary and secondary products of plant metabolism (McClure 1975).

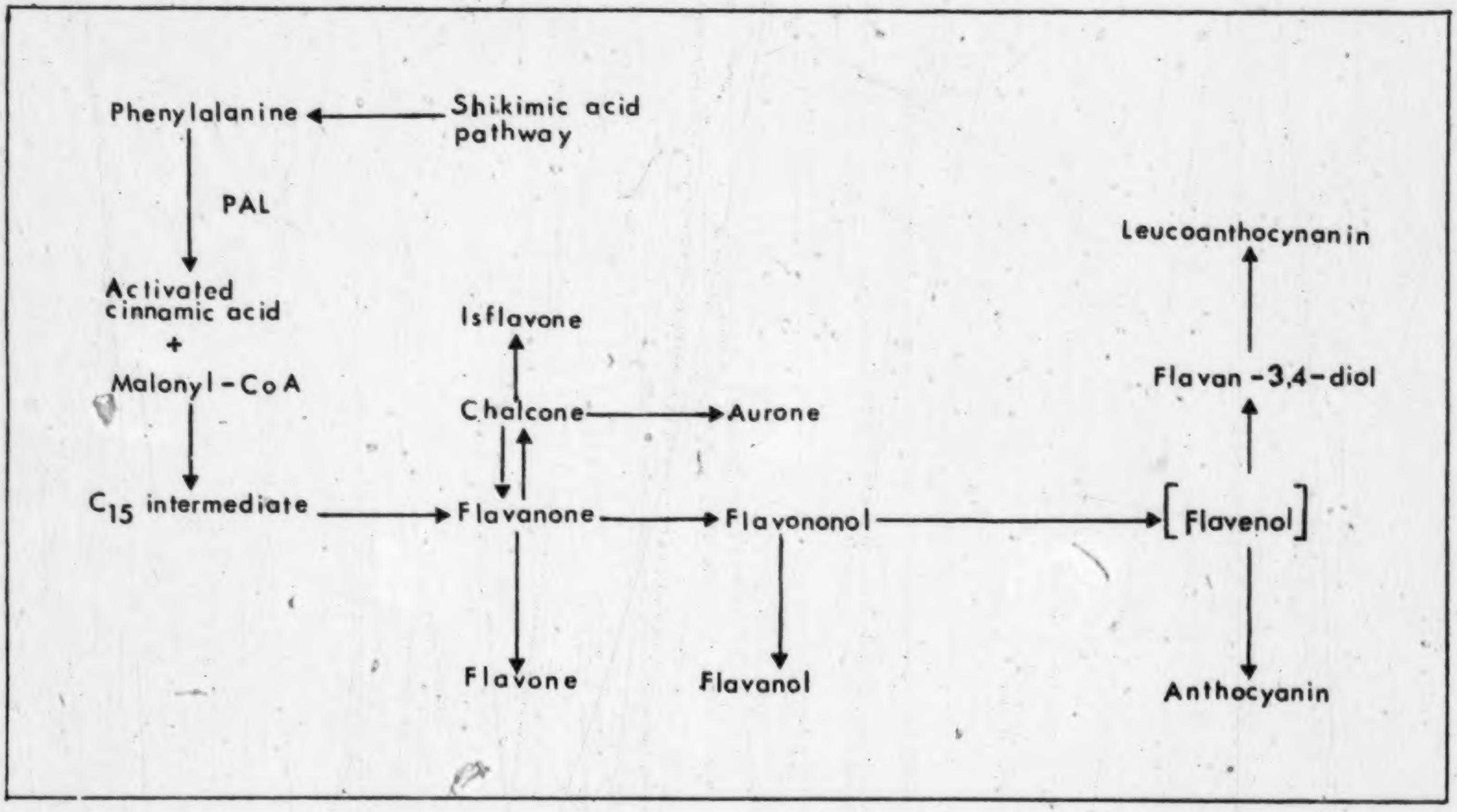
Phenylalanine
Shikimic acid pathway
PAL
Activated cinnamic acid
+
Malonyl-CoA
C_{15} intermediate
Isflavone
Chalcone
Aurone
Flavanone
Flavononol
Flavone
Flavanol
[Flavenol]
Leucoanthocynanin
Flavan-3,4-diol
Anthocyanin

Figure 6. Biosynthesis of flavonoid compounds (Harborne 1967).

this zone (Fahn 1973). The initiation of the separation layer is usually marked by the start of cell division which results in a layer about 2 to 3 cells wide of comparatively small, irregularly arranged, thin walled densely protoplasmic cells (Addicott 1945, Gawadi and Avery 1950, Webster 1970). A protective layer consisting of lignified and suberized parenchyma cells, develops below this area of separation to prevent dessication and entry of pathogens. The development of the separation and protective layers results in the entire abscission zone being approximately 12-16 cells in width.

The stimulus to initiate these anatomical changes effecting abscission, arise from the senescent cells of the leaf immediately distal to the cells of the abscission zone. Osborne (1973) states that it is not mandatory for the entire leaf be senescent in order to induce abscission.

During the actual process of separation a chemical alteration occurs in the walls of the cells of the abscission zone (Leopold 1971). Wall changes involved may be characterized by a hydrolysis of the walls themselves (Sampson 1918), a loss of cementing effectiveness of the middle lamella (Morre 1968, Webster 1968) or by a simple fracture of the vascular elements (Webster 1970). In summarizing relevent literature, Leopold (1971) states that wall degradation may first involve the synthesis of the enzyme, polygalacturonase, capable of attacking the pectins cementing the middle lamella, and/or the synthesis or release of cellulases capable of attacking the cellulosic fraction of cell walls.

C. Influence of Environmental Factors

Senescence and abscission are complex physiological processes sensitive to and influenced by many environmental factors, however the combined influences of decreasing daylength and low temperature appear to be the most important (Kramer and Kozlowski 1960). Many of the environmental factors that influence leaf abscission (see Table 3) do so by affecting biochemical changes associated with leaf senescence. As mentioned previously, leaf abscission ordinarily occurs only when there are evident signs of senescence (dela Fuente and Leopole 1968).

1. Temperature

Decreasing temperatures are important in inducing changes in pigments and other chemical compounds associated with autumnal leaf senescence (Olmstead 1951, Creasy 1074). In addition to direct effects on metabolism such as pigment synthesis and degradation, decreasing temperatures can also have an indirect effect by increasing transport of materials from the leaf (Kozlowski 1973).

The increase in foliar anthocyanins that occurs in some species in response to lowered temperatures have been explained by temperature regulated starch to sugar conversions (Creasy 1974). This idea is supported by the fact that sugars have frequently been shown to stimulate red color formation in isolated tissue experiments. In following senescence changes over time, several workers have observed direct parallel relationships between anthocyanin and carbohydrate levels (Harborne et al 1975). Creasy (1974) noted when Euonymus alata was exposed to low temperature and a short photoperiod for 30 days that there was an increase in anthocyanins, a decrease in chlorophyll, and a gradual increase in soluble carbohydrates.

The effects of low temperature on anthocyanin synthesis have also been attributed to effects on enzymes, in particular, phenyl-

Table 3: Effects of some environmental factors on the promotion and retardation of abscission (Addicott 1968).

Factors	→ Promotion ← Retardation
Temperature	
Moderate	→
Light frost	→
Extremes: heat or frost	←
Light	
Photosynthetic: moderate	→
deficiency or excess	←
Photoperiodic: long days	←
short days	→
Water	
Drought or flooding	→
High humidity	→
Gases	
Oxygen	→
$<$ 20% oxygen	←
Carbon dioxide	⇄
Ethylene	→
NH_3	→
Mineral and soil factors	
Nitrogen	←
Deficiencies of N, Zn, Ca, S, Mg, K, B, Fe	→
Salinity and alkalinity	⇆
Biotic factors	
Insect or fungus injury to leaf blade	→

alanine ammonium-lyase (PAL), controlling this biosynthetic system. As shown in Figure 6, PAL is the enzyme which catalyzes the deamination of L-phenylalanine to trans-cinnamic acid, one step in the snythesis of anthocyanins (Zucker 1972). Low temperature has often been shown to increase PAL activity (Creasy 1974, Harborne et al 1975). Creasy (1974) has sugested that the low temperature PAL regulatory mechanism used to explain hydroxylated cinnamic acid production in gherkin seedlings (Engelsma 1970), may also explain autumnal coloration. In this biological system, an increase in PAL activity takes place in the course of exposure to temperatures 10°C or lower. Engelsma (1970) explains that at temperatures above 10°C, a PAL inactivating system compensates for PAL synthesis and that the end products (hydroxycinnamic acids) of the reaction catalyzed by PAL are involved in the induction and/or functioning of the inactivating system. It is inferred that as a consequence of the lower rate of synthesis of hydroxycinnamic acids at lower temperatures which prevents their build up, newly synthesized PAL is not inactivated and that previously synthesized PAL is released from an enzyme - inactivation complex.

The process of abscission is also influenced by temperature and requires moderate temperatures to proceed in a normal fashion (Addicott 1968). Frequently, a light frost will initiate abscission. On the other hand, uncommonly low temperatures, such as a heavy frost, will often damage the abscission zone so severely that the process cannot take place (Addicott 1968).

2. Light

Light intensity, quality and duration all influence anthocyanin formation, chlorophyll degradation and subsequent leaf abscission (Addicott 1968). Light intensity plays a major role in determining the carbohydrate status of senescing tissue by influencing photosynthesis. Carbohydrates, are necessary for abscission (Biggs and Leopold 1957) but either a deficit below or an excess above that required for growth will slow the process (Addicott 1968). Biggs and Leopold (1957) explain that the abscission inhibiting effect of excessive carbohydrate is due to the fact that the carbohydrates of photosynthesis are utilized directly for deposition of cell walls. When environmental factors combine to favor photosynthesis (ie. long days and/or high light intensity) but to restrict overall growth (ie. low temperature), cell walls become heavier and abscission is more difficult. Presumably, in cases where carbohydrate levels are insufficient for growth, there is also insufficient carbohydrate to meet the energy requirements for synthesis of enzymes involved in abscission.

Light intensity and light quality have been reported as influencing numerous stages of the complex process of anthocyanin synethsis in a wide range of plants (McClure 1975). However, few generalizations on the photocontrol of anthocyanin synthesis can be made. McClure (1975) believes most light quality responses are explainable on the basis of one of four classes of photoreaction:

1) the low energy requiring, red, far-red reversible phytochrome system.
2) a high irradiance response that is satisfied with one joule cm^{-2} of either far-red or blue light.
3) photosynthetic involvement in precursor or cofactor production.

4) complex responses that work indirectly through enhanced growth hormone synthesis.

Duration of the light period, has a sizeable effect on the induction of pigment changes associated with leaf senescence and subsequent abscission. Senescence and abscission can be delayed when the natural autumnal daylength is extended by supplemental illumination and can be hastened by short day treatments (Wareing 1956). Vince-Prue (1975) reports that anthocyanin synthesis in leaves of many plants is influenced by photoperiod, although the controlling mechanism was not always the same in the few plants studied. For example, anthocyanin formation in leaves of Kalanchöe, Kalanchöe blossfeldiana seems to be under the control of daylength in a manner similar to flowering; short days initiating flowers and increasing anthocyanin production (Neyland et al 1964). In contrast to Kalanchöe, anthocyanin content in leaves of the short day plant, Perilla was decreased by short days. Furthermore, the fall in anthocyanin content did not necessarily accompany the induction of flowers in short days (Shumacker 1966). Therefore, in Perilla, anthocyanin synthesis is not correlated with flowering as it is in Kalanchöe and is thus controlled differently. Plants responding to long days by producing more anthocyanin than when exposed to short days may not necessarily be exhibiting a photoperiodic response but may be responding to an increase in total quantity of light received (Vince-Prue 1975).

D. Internal Regulation

It has been theorized that environmental factors effect senescence by inducing changes in phytohormone levels (Kozlowski 1971). For example, in most woody perennials, auxin and gibberellin levels are high, and concentrations of inhibitors such as abscisic acid, are low under long days. The converse is true under short days. The long days of spring and summer are presumed to maintain auxin and gibberellin contents at a level high enough to prevent senescence (Nitsch 1963).

Leaf age is also important with respect to the presence of phytohormones. Wetmore and Jacobs (1953) have shown in leaves of Coleus, Coleus blumei, that the older the leaf, the lower its content of extractable and diffusible auxin. Osborne (1973) suggested that by late summer, the leaves of a deciduous tree could be of an age when auxin levels are falling. It has been shown that application of either auxin or gibberellin to green leaves in autumn will retard their senescence (Osborne 1959, Osborne and Hallaway 1960).

The effect of changes in phytohormone levels on some individual senescence processes have been isolated. With respect to autumn coloration, Lee and Tukey (1971) and Hemphill and Tukey (1973), noted in Burning Bush, Euonymus alata that repeated sprays with abscisic acid increased coloration. Brian et al (1959) observed that autumnal coloration and leaf fall of some deciduous tree species can be delayed by spraying with gibberellic acid. High levels of cytokinins have also been found to delay chlorophyll degradation and the decline in DNA and RNA content associated with senescence. These affects of cytokinins have been ascribed to protein and amino acid accumulation (Mothes et al 1959, Osborne 1965, Shiboaka and Thimann 1970, Skoog and Armstrong 1970). Barmore (1975) found that increased levels of ethylene during senescence were associated with increased rates of chlorophyll degradation. He explains this phenomena on the basis of a measurable increase in synthesis and/or activity of chlorophyllase and other enzyme systems which could alter the structural integrity of chloroplast units.

The photocontrol of PAL has been extensively studied in an attempt to understand anthocyanin synthesis. The synthesis of PAL in etiolated seedlings has been shown to be a low energy requiring red, far-red reversible response or a high irradiance response (Zucker 1972). PAL synthesis in green leaf tissue, however, is often controlled by photosynthesis (Zucker 1969, Duke et al 1976). Zucker (1972) and Camm and Towers (1973) state that although the variety of light factors influencing PAL activity usually stimulate phenolic production, the correlation between PAL induction and phenolic biosynthesis cannot be established in all situations.

PAL levels in a variety of tissues have also been shown to be affected by endogenous hormonal levels and by exogenous application of hormones. For example, Walton and Sondheimer (1968) noted that abscisic acid influences development and retention of PAL activity in excised pea axes. Camm and Towers (1973) reported that exogenous ethylene usually increases PAL activity in a large number of plants. Leonova and Gamburg (1972) found NAA markedly decreased PAL activity in tobacco, Nicotiana tabacum. However, once again, the variety of hormonal factors affecting PAL levels do not always have a corresponding affect on anthocyanin levels (McClure 1975).

Although many hormonal changes influencing leaf senescence such as the ones described have been measured, the actual stimulus originating in senescent tissue to induce leaf abscission is ethylene (Abeles and Rubenstein 1964, Burg 1968, Webster 1970, Leopold 1971, Osborne 1973). In all species studied by these researchers, where ethylene production has been monitored, the tissues distal to an abscission zone have been found to produce relatively large amounts of gas during senescence and prior to leaf abscission. Applied ethylene has also been shown to accelerate petiole senscence (Abeles et al 1971). The action of ethylene is believed to be involved with stimulatory release of enzymes responsible for structural deterioration of the separation layer (Abeles 1968, Abeles and Holm 1968, Beyer 1975).

Auxin is believed to interact with ethylene in controlling leaf abscission (Leopold 1971). Its effect has been to delay or negate the abscission accelerating role of ethylene. This is achieved by maintaining the abscission zone in an immature condition (Gawadi and Avery 1950, Abeles et al 1971) or by preventing the cells below the zone from responding to the ethylene stimulus (Webster 1970).

Other phytohormones such as gibberellic and abscisic acid are known to influence leaf abscission (Chatterjee and Leopold 1964). Their effects can also be explained by their interaction with ethylene. Morgan and Durham (1975) have presented an hypothesis for possible interaction of gibberellins and ethylene in abscission. They suggest that ethylene initiates anatomical changes associated with abscission but that it is gibberellic acid that promotes the division of cells associated with the formation of the separation layer. Abscisic acid, on the other hand, has been observed to enhance the senescence of tissue distal to the abscission zone and thus promote ethylene production but, according to Morgan and Durham (1975), it is less effective in this regard than gibberellic acid.

MATERIALS AND METHODS

I. Plant Materials

The *Euonymus alata* Sieb. 'Compacta' plants used in these studies were obtained bare root from Sheridan Nurseries (Etobicoke, Ontario). The plants, of two distinctly different lots, were designated as either Eastern or Western grown. Eastern grown (EG) plants were received during April, 1976. They were approximately 38-46 cm tall and were 3 years old. Western grown (WG) plants were 3 years old when received during April, 1973. They were then grown under Edmonton conditions from April, 1973 to April, 1976.

Twenty EG plants and five WG plants were planted outdoors (south end of block 5, Parkland Farm, University of Alberta). Eighty EG plants were potted up in 35 cm diameter pressed cardboard pots using University of California mix (Baker 1957, p. 134) as the growing medium.

After planting, all plants were pruned to leave 7-9 shoots, uniform in height and diameter, to facilitate more uniform light penetration and thus lessen sample variability.

The potted plants were placed in a greenhouse under natural photoperiodic conditions. Temperatures of 18°C (day) and 16°C (night) were maintained. From August 5, 1976 onward, daylength was extended to 20 hours with artificial light.

II. Experimental Methods

A. Effects of Environmental Factors on Leaf Morphology

1. Eastern and Western Environments

Because noted morphological differences were common between

EG and WG plants, sections of tissue were taken from mature leaves to determine if there was any observable anatomical differences.

2. Temperature and Photoperiod

Five treatments were used to determine if the difference in Eastern and Western conditions (photoperiod and temperature) had any influence on producing the observed differences in leaf morphology between Eastern and Western grown plants (see Table 4). The treatments were carried out under controlled environment conditions (Environmental Growth Chambers, Chagrin Falls, Ohio).

Ten dormant, potted EG plants were used per treatment. The plants were artificially induced to break dormancy and initiate new leaf growth under treatment conditions. This was achieved by exposing them to 4°C for 8 weeks just prior to the start of treatment. The plants were fertilized with 380 ml of 1.6 g l^{-1} of 20-20-20 fertilizer solution at the first sign of bud break and at monthly intervals thereafter. Regular spraying with Kelthane WP was needed to control spider mite populations.

The first and second treatments were designed to test the effect of Eastern and Western temperatures during the growing season on leaf morphology. The maximum and minimum temperatures normal[1] for June in Edmonton (20°C/7°C) were used to simulate temperatures of the Western growing season.

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[1] Normal values throughout this entire study are based on the period 1941-1970 (Environment Canada 1971).

Table 4. Treatments used to determine the effect of Eastern and Western temperatures and photoperiods on leaf morphology.

Treatment No.	Conditions Simulated	Temp$^+$ °C	Photoperiod hr	PAR^{++} $\mu Em^{-2}s^{-1}$	Light values incident to the treatment Illuminance (klux)	 Blue 400-500 nm $\mu W\ cm^{-2}nm^{-1}$	 Red 600-700 nm $\mu W\ cm^{-2}nm^{-1}$	 Far-Red 700-800 nm $\mu W\ cm^{-2}nm^{-1}$
1	Western temperatures Eastern photoperiod	20/7	16	420	30	12.0	11.0	5.5
2	Eastern temperatures Western photoperiod	23/13	16	420	30	12.0	18.0	5.2
3	Western temperatures Eastern photoperiod	20/7	16	380	26	12.0	14.0	5.5
4	Western temperatures Western photoperiod	20/7	18	380	26	12.0	23.0	5.2

+ Starting at the beginning of the light period, plants were exposed to 18 hours of the higher temperature followed by 6 hours of the lower temperature.

++ PAR = photosynthetically active radiation; measured between 400 and 700 nm.

Averages of the maximum (23°C) and minimum temperature norms (13°C) for June, in Toronto and Ottawa were used to simulate growing season temperatures of Eastern Canada. Plants in both treatments were exposed to a 16 hour photoperiod.

Treatments 1 and 4 were used to determine the effect of Eastern and Western photoperiods (16 and 18 hours respectively) on leaf morphology when temperatures were held at 20°C/7°C. Eighteen hours is the average daylength during June in Edmonton and 16 hours is the average daylength during June in Ottawa and Toronto. The level of photosynthetically active radiation (PAR) in the Western photoperiod treatment was 380 microeinsteins meter^{-2} second $^{-1}$ (380 μE m^{-2} s^{-1}) while that of the Eastern photoperiod treatment was 420 μE m^{-2} s^{-1}. The level of PAR in the 18 hour photoperiod treatment was reduced so that the total quantity of PAR received per day by the plants was identical in both treatments.

Treatments 1 and 3 were compared to see what effect the reduced light intensity in Western photoperiod treament might have on leaf morphology. Five mature leaves from each treatment were sampled for anatomical observation. Leaves were considered to be mature when shoot elongation had ceased. It was assumed that elongation had ceased with the appearance of a terminal bud. Thickness of the leaves, formed under the various treatments, was also measured using a micrometer with a vernier scale reading to 4 decimal places.

Leaves from plants in all treatments were also sampled for chlorophyll analysis.

B. Effects of Environmental Factors on Senescence Phenomena

1. Temperature

a. Field Experiments

The effect of autumnal temperatures on chlorophyll degradation, anthocyanin accumulation, ∝-amino nitrogen content, and abscission layer formation was observed in the field grown plants. Twenty (EG) field plants were used for these measurements.

The effect of temperature on pigment changes were studied from September 17, 1976 to November 8, 1976 to determine if the relatively cool Western autumnal temperatures adversely affected typical bright red autumn coloration. The effects of temperature on ∝-amino nitrogen content of leaves and on abscission layer formation were studied to determine whether or not other senescence processes were influenced by the cooler temperatures.

During this same period, temperatures to which six field plants were exposed, were modified to slightly raise the minimum daily temperature. This was achieved by covering the plants in this treatment each day at sunset with insulated covers. The covers were removed daily just prior to sunrise. A small heater was also placed under the cover. Heaters consisted of a single 100 W incandescent light bulb surrounded by a sleeve of sheet metal 25 cm long and closed at the top with black cloth to ensure complete darkness. The heaters were thermostatically controlled to operate whenever temperatures at plant level fell below 5°C. Five°C is the average of the minimum temperature norms for October in Toronto and Ottawa.

Temperature measurements were recorded on the third pair of leaves below the terminal bud of plants in both the modified and noncontrolled temperature-field treatments. Copper-constantan thermocouples, with junctions made of 0.076 mm copper and constantan wires (Omega Engineering, Stamford, Conn.) attached to 0.25 mm stainless steel wire clips (see Appendix 3), were fastened to the abaxial leaf surface. Ten centimeters from the junction, the wires were joined to 1 m of 0.127 mm thermocouple lead wire (Omega Engineering, Stanford, Conn.). This lead wire was then attached to 12 m of 8 mm thermocouple lead wire (Thermoelectric, Calgary, Alberta) which led to a Honeywell Electronic, 24 channel, stripchart recorder.

Temperature was continuously recorded during the period September 17, 1976 to November 8, 1976. Samples for analysis of anthocyanin, chlorophyll and α-amino nitrogen were collected at intervals during this period from plants of both temperature treatments. Sampling was discontinued on November 8, 1976 because the large number of abscised leaves prevented the collection of representative samples. Samples for examination of abscission zone formation were taken on November 1, 1976 from plants in both the modified and non-controlled temperature treatments. For comparative purposes, samples were also taken from non-senescent leaves of EG potted plants and from senescent leaves of EG potted plants that were more highly colored than those from either field temperature treatment.

b. Controlled Environment Experiments

Controlled environment studies of the effect of temperature on chlorophyll degradation and anthocyanin accumulation were carried out in growth chambers. These were undertaken to provide more information on the influence of autumn temperatures on leaf coloration (see Table 5). Ten EG potted plants were used in each treatment.

Table 5. Treatments used to determine the effect of temperature on chlorophyll degradation and anthocyanin accumulation during a constant 13 hour photoperiod.

Treat No.	Autumn Conditions Simulated[+]	Date Started	Temperature[++] (°C)
1	Maximum and minimum temperatures normal for Eastern Canada	Nov. 22	15/5
2	Maximum and minimum temperatures normal for Western Canada	Nov. 22	15/2 for the first 31 days then 15/0/-5 for 19 days
3	Maximum temperature normal and minimum temperature intermediate to those normal for Eastern and Western Canada.	Oct. 6	15/2
4	Maximum and minimum temperatures higher than normal in both Eastern and Western Canada	Oct. 6	18/10

[+] Chambers were lit with eight equally spaced cool white fluorescent lamps (Sylvania F96T10/CW) which provided, at mid-plant height; PAR (400-700 nm) - 55 $\mu E\ m^{-2}\ s^{-1}$; total irradiance - 10 $W\ cm^{-2}$, illuminance 2500 lux, red radiant energy (600-700 nm) 1.4 $\mu W\ cm^{-2}\ nm^{-1}$ and blue radiant energy (400-500 nm) - 1.9 $\mu W\ cm^{-2}\ nm^{-1}$.

[++] Starting at the beginning of the light period plants were exposed to 18 hours of the higher temperature followed by 6 hours of the lower temperature.

Treatments 1 and 2 were designed to simulate October temperatures in Eastern and Western Canada respectively. Treatment 3 provided a maximum temperature, normal to both regions, but a minimum temperature that was intermediate to those normal for both regions. Treatment 4 provided maximum and minimum temperatures both higher than normal for both regions.

Temperatures were based on those normal for October because the rates of chlorophyll degradation and anthocyanin accumulation are greatest during this period. The 13 hour photoperiod, used in all treatments, is the average daylength in both regions during the last half of September and the early part of October.

2. Photoperiod

Controlled environment studies to observe the effect of photoperiod on chlorophyll degradation and on anthocyanin accumulation, when temperatures were held at 15°C/2°C, were carried out in growth chambers (see Table 6).

Treatments 1 and 2 (an 18 and a 13 hour photoperiod respectively) were used to see whether or not the senescent responses of E. alata Sieb. 'Compacta' were sensitive to photoperiod. Ten EG potted plants were used in each treatment.

Treatments 3 and 4 simulate autumnal daylength changes in Western and Eastern Canada respectively. The ten potted plants used in each of two treatments had a slightly different environmental background than the plant material used in Treatments 1 and 2, therefore Treatments 3 and 4 can be validly compared only with one another.

Table 6. Treatments used to determine the effect of photoperiod on chlorophyll degradation and anthocyanin accumulation. Temperatures held constant at 15°C/2°C.+

				LIGHT VALUES INCIDENT TO THE TREATMENT+++			
Treatment No.	Treatment Description	Daylength++ hrs.	PAR $\mu Em^{-2}s^{-1}$	Illuminance Klux	Total Irradiation Wm^{-2}	Blue 400-500nm $\mu W\ cm^{-2}nm^{-1}$	Red 600-700nm $\mu W\ cm^{-2}nm^{-1}$
1	Long Photoperiod	18	55	2.5	10.0	1.9	1.4
2	Short photoperiod	13	55	2.5	10.0	1.9	1.4
3	Western conditions	18 for 2 weeks then 13	130	7.0	30.0	3.5	2.9
4	Eastern conditions	13	130	7.0	30.0	3.5	2.9

+ Starting at the beginning of the light period, plants were exposed to 18 hours of the higher temperature followed by 6 hours of the lower temperature.

++ Daylength was based on a high intensity light period of 13 hours. This basic light period was extended with 1.0 mW cm^{-2} (200 lux) of light from incandescent lamps.

+++ Levels of far-red radiation too low to be measured ($<0.5\ \mu W\ cm^{-2}\ nm^{-1}$).

Daylengths of 16-18 hours persist in Western Canada for 2 weeks longer in the fall than in Eastern Canada. Thus, the 18 hour daylength assigned at the start of Treatment 3 was used to simulate this condition. The subsequent 13 hour daylength was used to simulate the light period occurring later in autumn (September 15-October 1) in both regions.

3. Light Quality

Two light treatments were used to see whether or not the ratio of far-red:red light influenced chlorophyll degradation and anthocyanin accumulation in *E. alata* Sieb. 'Compacta' (Table 7). Temperatures during treatment were held constant at 15°C/2°C and daylength was maintained at 13 hours. Five EG potted plants were used in Treatment 1 and, due to a larger growth chamber, ten plants from the same source were used in Treatment 2.

In these experiments no attempt was made to simulate light quality conditions from either Eastern or Western Canada.

4. Senescence Responses of Leaf Types

a. Field Experiments

The effect of Edmonton autumnal temperatures, occurring during the period September 17, 1976 to November, 1976, on chlorophyll degradation and anthocyanin accumulation was observed on five WG *E. alata* Sieb. 'Compacta' plants in the field as well as on the EG plants described previously. This was done to determine if pigment changes during senescence were similar in the two distinctly different leaf types.

Table 7. Treatments used to determine the effect of the far-red:red light ratio on chlorophyll degradation and anthocyanin accumulation. Temperatures held at 15°C/2°C+, photoperiod 13 hours.

					LIGHT VALUES INCIDENT TO THE TREATMENT		
Treatment No.	Far-red: red-light ratio	Far-red light 700-800 nm $\mu W\ cm^{-2}\ nm^{-1}$	Red light 600-700 nm $\mu W\ cm^{-2}\ nm^{-1}$	PAR $\mu Em^{-2}s^{-1}$	Illuminance Klux	Total Irradiation $W\ m^{-2}$	Blue light 400-500 nm $\mu W\ cm^{-2}\ nm^{-1}$
1	0.0	<0.5++	1.4	55	2500	10.0	1.9
2	0.77	1.7	2.2	55	3600	50.0	1.7

+ Starting at the beginning of the light period, plants were exposed to 18 hours of the higher temperature followed by 6 hours of the lower temperature.

++ Below the range of sensitivity of the measuring instrument.

b. Controlled Environment Experiments

To supplement field experiments, the senescence responses of both Eastern and Western leaf types were studied in controlled environments. To avoid digging and potting up field plants, cuttings from EG and WG plants were used in these experiments. Twenty, 15 cm long cuttings were taken from terminal shoots of each plant type on August 9, 1978 and placed in a mist propagation bench. On October 15, 1976 the rooted cuttings were potted up in 10 cm pots using University of California mix as the medium. The cuttings were then exposed to temperatures of 15°C/2°C and a 13 hour photoperiod (PAR-55 $\mu E\ m^{-2}\ s^{-1}$). Other light values incident to the treatment included: total irradiation -10.0 $W\ m^{-2}$, illuminance-2500 lux, red light (600-700 nm)-1.4 $\mu W\ cm^{-2}\ nm^{-1}$ and blue light (400-500 nm)-1.9 $\mu W\ cm^{-2}\ nm^{-1}$.

Experiments were also conducted to determine whether or not any possible difference in autumn coloration between Eastern and Western leaf types was due to the photoperiod and temperature under which they were formed (see Table 8). The ten EG potted plants used in each treatment were grown for one season under the temperature and daylength combinations described in Table 8. When the leaves of the plants in each treatment were mature, they were induced to senesce by decreasing both the daylength and temperature. Leaves were considered mature when shoot elongation had ceased. Elongation was said to have ceased with the appearance of a terminal bud. Leaf samples were taken during the senescence period for chlorophyll and anthocyanin evaluation.

Table 8. Treatments used to determine the combined effect of photoperiod and temperature during leaf formation on leaf senescence responses.

Treatment no.	Conditions under which leaves were formed	Conditions under which leaves of all treatments were induced to senesce							
		Established levels			Light levels incidental to treatment				
1	Western temperatures (20°C/7°C)+ Eastern daylength (16 hr)	Temperature - 15°C/2°C	Photoperiod - 13 hr	PAR - 130 $\mu E\ m^{-2}\ s^{-1}$	Illumination - 7.0 klux	Total Irradiation - 30.0 $\mu W\ m^{-2}$	Blue light - 3.5 $\mu W\ cm^{-2}\ nm^{-1}$	Red light - 2.9 $\mu W\ cm^{-2}\ nm^{-1}$	Far-red light - 0.5 $\mu W\ cm^{-2}\ nm^{-1}$
2	Western temperatures (20°C/7°C)+ Western daylength (18 hr)								
3	Eastern temperatures (23°C/13°C)+ Eastern daylength (16 hr)								

+ Starting at the beginning of the light period, plants were exposed to 18 hours of the higher temperature followed by 6 hours of the lower temperature.

III. Analytical Methods

A. Sampling Procedures for Chlorophyll and Anthocyanin Evaluation

Five samples, each consisting of ten randomly chosen disks cut from leaf tissue with a cork borer, were taken for chlorophyll analysis. In order to minimize sample variability, only the second and third pairs of leaves distal to the terminal bud were sampled. An identical sampling procedure was followed for anthocyanin analysis. When immediate analysis was not possible, leaf disks for chlorophyll determination were stored under nitrogen at -30°C and leaf disks for anthocyanin determination were stored in 1% HCl at -30°C.

When chlorophyll and anthocyanin were expressed on a dry weight basis as well as on an area basis, five additional samples were taken and dried for 10 hours at 100°C. The weight of these additional samples was used in calculating both chlorophyll and anthocyanin content on the basis of tissue dry weight.

B. Chlorophyll Extraction and Analysis

Each sample was ground with 30 ml of 80% acetone for 10 minutes at medium speed in a Virtis high speed homogenizer. After vacuum filtration, a petroleum ether separation was carried out to separate the water soluble anthocyanins from the ether soluble chlorophylls. The ether extract was evaporated to near dryness, using a flash evaporator at 40°C, then redissolved in a known volume of 80% acetone for spectrophotometric analysis.

Absorbance was read on a Bausch and Lomb Spectronic 20 spectrophotometer at 645 and 663 nm. The equations of Arnon (1949) were used in calculating chlorophyll a, b, and total chlorophyll concentrations which were reported as mg cm^{-2} of leaf tissue. Where sample weight was also recorded, chlorophyll concentration was expressed as mg g^{-1} of dry leaf tissue. Sestak et al (1971) recommend expressing chlorophyll content both ways as some variations in chlorophyll content, when expressed as mg cm^{-2} leaf tissue, are more readily explainable by differences in sample weight.

C. Anthocyanin Extraction and Analysis

Each sample was ground with 30 ml of 1% HCl for 10 minutes at medium speed in a Virtis high speed homogenizer. After vacuum filtration the extracts were made to a volume of 50 ml and absorbance was measured with a Bausch and Lomb Spectronic 20 spectrophotometer at 512 nm, the wavelength of maximum absorption. The absorbance spectrum of an anthocyanin extract in 1% HCl as measured by the scanning mode of a Beckman DB-G spectrophotometer (Beckman Instruments Inc., Fullerton, California) is shown in Figure 7.

Fuleki and Francis (1968) suggest that the best way to report anthocyanin measurements is to express the results in terms of the absolute quantities of each anthocyanin present in the extract. For this it is necessary to establish not only the identity and relative quantity of each pigment in the extract but also their individual extinction coefficients in the solvent used. The only known anthocyanin in E. alata Sieb. 'Compacta' is cyanidin-3-monoglucoside (Ishikura 1972). The only reported extinction coefficient for a cyanidin derivative in 1% HCl is for cyanidin-3-rhamnoside glucoside (Jorgensen and Geissman 1955): molecular weight 650.5, absorption maximum 512 nm, molar extinction coefficient 2.82×10^4.

It is difficult to prepare crystalline anthocyanin free of impurities and in sufficient quantities to permit the several weighings

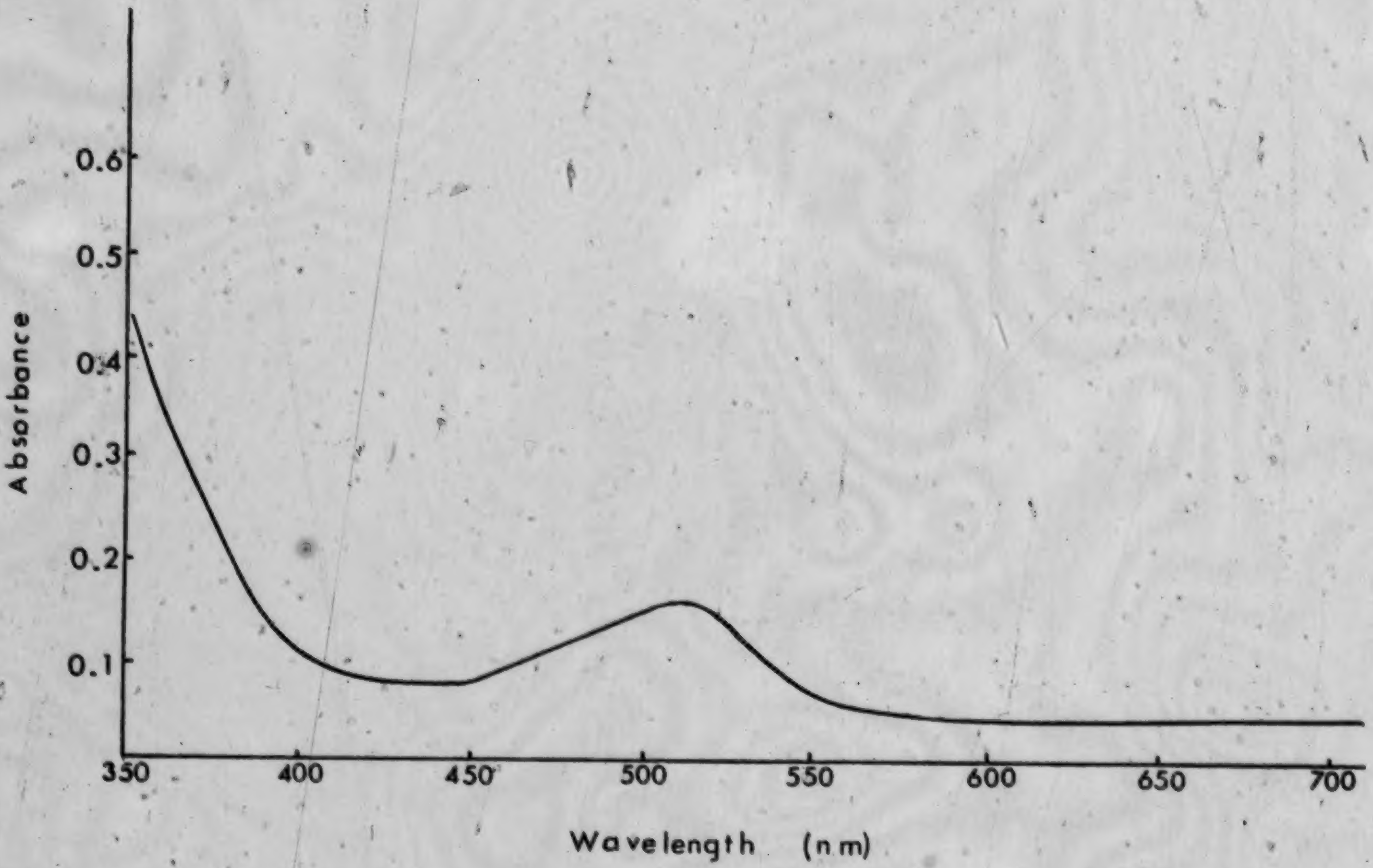


Figure 7. Absorbance spectrum of a 1% HCl extract of *E. alata* Sieb. 'Compacta' leaves as measured by a scanning spectrophotometer.

necessary to determine an extinction coefficient. For this reason the extinction coefficient for cyanidin-3-rhamnoside glucoside (cy-3-rh glu) was used in determing absolute anthocyanin levels. Fuleki and Francis (1968) state that use of a closely related anthocyanin is sufficiently accurate for comparative purposes.

The following method was used in calculating absolute anthocyanin levels from measurements of absorbance (Fuleki and Francis 1968).

$$A = abc$$

A = absorbance (optical density)

a = molar extinction coefficient (absorbance mole^{-1})

b = pathlength (cm)

c = concentration (mole liter^{-1})

As b = 1 cm and absorbancies of solutions are expressed as having passed through a 1 cm pathlength;

$$\text{then, } c = \frac{A}{a}$$

To express concentration in g rather than in moles;

$$c = \frac{A}{a} \times \text{molecular weight}$$

All absorbancies were expressed on the basis of a 50 ml extract;

$$\text{hence, total anthocyanin} = c \times .050\ 1$$

$$= x\ \text{g}$$

Since the total area of tissue from which the anthocyanin extracted was known;

$$\text{then, total anthocyanin} = x\ \text{g} \div y\ \text{cm}^2$$

$$= z\ \text{g cm}^{-2} \text{ or } z \times 10^{-6}\ \mu\text{g cm}^{-2}$$

D. α-Amino Nitrogen Extraction and Analysis

Leaf tissue samples taken with a cork borer were immediately frozen in liquid nitrogen and stored at -40°C until analysis.

The extraction procedure followed was that of Lee and Tukey (1971) with minor alterations. Each sample was ground at low speed on a Virtis blender three times for 30 minutes each with 20 ml of hot ethanol. The resulting extracts were centrifuged, combined, dried in vacuo at 40°C, and redissolved in 15 ml of ethanol.

The extracts were desalted according to the following method modified from Plaisted (1958b). Dowex 50-X8, 100-200 mesh, H^+ was prepared for use by washing with water five times. After each wash the heavy particles were allowed to settle and the fine material was decanted off. The resin remaining was then poured into a 500 ml burette with a glass wool plug in the outlet and the following solutions were passed through in sequence three times;

1. 10% sodium chloride solution (W/V) until the effluent showed neutral reaction with pH indicator paper.
2. 300 ml deionized water.
3. 2N HCl until the effluent showed an acid reaction with pH indicator paper.
4. deionized water until the effluent showed a neutral reaction with pH indicator paper.

After the last water wash the resin was soaked and stored in 80% ethanol until use.

Exchange columns, 1 cm in diameter and 5 cm in height, were prepared by washing the resin into the columns with 80% ethanol. After the resin had settled, a small plug of glass wool was placed on top of the column. The resin was kept moist at all times with 80% ethanol.

The ethanolic amino acid extract was passed through the column at the rate of 2 ml of liquid per minute. Twenty ml of 80% ethanol was added to the column to rinse the resin. The amino acids were eluted from the column by the following procedure and eluates were collected;

1. 40 ml of 0.4 N ammonium hydroxide in ethanol
2. 15 ml of 80% ethanol
3. 15 ml of distilled water
4. 15 ml of 4.0 N ammonium hydroxide
5. 15 ml of distilled water

Columns were prepared for reuse by following the previously described washing procedure. Eluates were dried in vacuo at 40°C and quantitatively redissolved in 1.5 ml of 10% i-propanol. Samples were stoppered with corks treated with a solution of 2% citric acid in ethanol, to prevent uptake of ammonia (Moore and Stein 1954), and stored in the dark at -40°C until analysis.

Soluble α-amino nitrogen was determined photometrically using the ninhydrin-hydrindantin reagent of Moore and Stein (1954). Blanks were prepared for use in the photometric analysis by passing 15 ml of 80% ethanol through the columns and following the same elution procedure used in sample analysis. A standard curve was constructed (see Appendix 5) using a 1.0 mM stock solution of alanine in 0.1 M citrate buffer at pH 5.0 (Lee and Tukey 1971). Results were expressed as μg of alanine cm^{-2} leaf tissue.

E. Anatomical Investigations

Samples taken for study of abscission zone consisted of a leaf petiole and a small piece of stem tissue surrounding the base of the petiole. Samples taken for leaf anatomical studies consisted of a 0.3 cm by 1.0 cm piece of leaf blade tissue. All samples were taken from the third pair of leaves distal to the terminal bud.

To stop protoplasmic activity, tissue was fixed in Randolph's (1935) modified Navashin fluid immediately after sampling. The fixed samples were then vacuum infiltrated in the fluid for 24 hours, and washed for 12 hours in cold, slowly running water. Dehydration was carried out by soaking the tissue consecutively in solutions of 10%, 20% and 30% ethanol followed by the tertiary butyl alcohol series of Johansen (1940). The tissues were then infiltrated with and embedded in parowax. To avoid tissue tearing of the relatively woody abscission zone samples, the parowax blocks were soaked for five days in a 4% Tween solution. Longitudinal sections of the abscission zone tissue and transverse sections of the leaf tissue, 8-10 µ thick, were made with a rotary microtome. The sections were attached to slides with Haupt's adhesive and deparaffinized according to the method of Johansen (1940).

Abscission zone samples were stained using the safranin - Heidenhain's haematoxylin method of Esau (1944). For details see Appendix 4. Tissues were then viewed under polarized light to determine the cellulosic content of cell walls. Only crystalline materials such as cellulose, which are birefringent, are visible under polarized light.

Leaf tissue samples were stained using the safranin-fast green schedule of Johansen (1940). After mounting, slides of both abscission zone and leaf tissue were examined and photographed on a photomicroscope at magnifications of 40x, 64x, 100x and 252x.

F. Light Measurements

PAR (400-700 nm), total irradiance, and illuminance were measured with a cosine corrected, Lambda model L1-185 quantum/radiometer/photometer. Blue (400-500 nm), red (500-600 nm) and far-red (600-700 nm) light energy was measured with a Plant Growth Photometer, model 1L-150 (International Light Inc., Dexter Industrial, Newburyport, Mass.).

RESULTS AND DISCUSSION

I. Effects of the Eastern and Western Environment on Leaf Morphology

Marked differences in leaf morphology of EG and WG field plants were evident from visual examination. Leaves of EG plants appeared slightly larger, lighter green, and thinner than leaves of WG plants. These observations are supported by Knowles (personal communication) who has observed plants growing in both Southern Ontario and Edmonton.

In these experiments both leaf types expanded and matured under identical growing conditions, therefore the observed differences in leaf morphology were obviously due to environmental influences from the previous season. The greater thickness of leaves of WG plants was largely due to an increased amount of palisade parenchymatous tissue. Palisade parenchyma in leaves of WG plants was, on the average, five to seven cell layers thick as compared to being two cell layers thick in leaves of EG plants (see Figures 8-1 and 8-2).

Other anatomical differences between the leaves of WG and EG plants were also observed. The cuticle of leaves of WG plants appeared thicker than that of leaves of EG plants and cells of the palisade parenchyma of leaves of WG plants appeared also to contain more deposits of darkly stained material. The latter was not identified but was most likely tannin (Esau 1965).

The observed differences in leaf anatomy are characteristic of the differences between "sun" and "shade" leaves. Leaves produced under high light intensity ("sun" leaves) have a larger amount of palisade parenchymatous tissue than leaves produced under low light intensity [("shade leaves"), Wylie 1949, Talbert and Holch 1957, Kramer

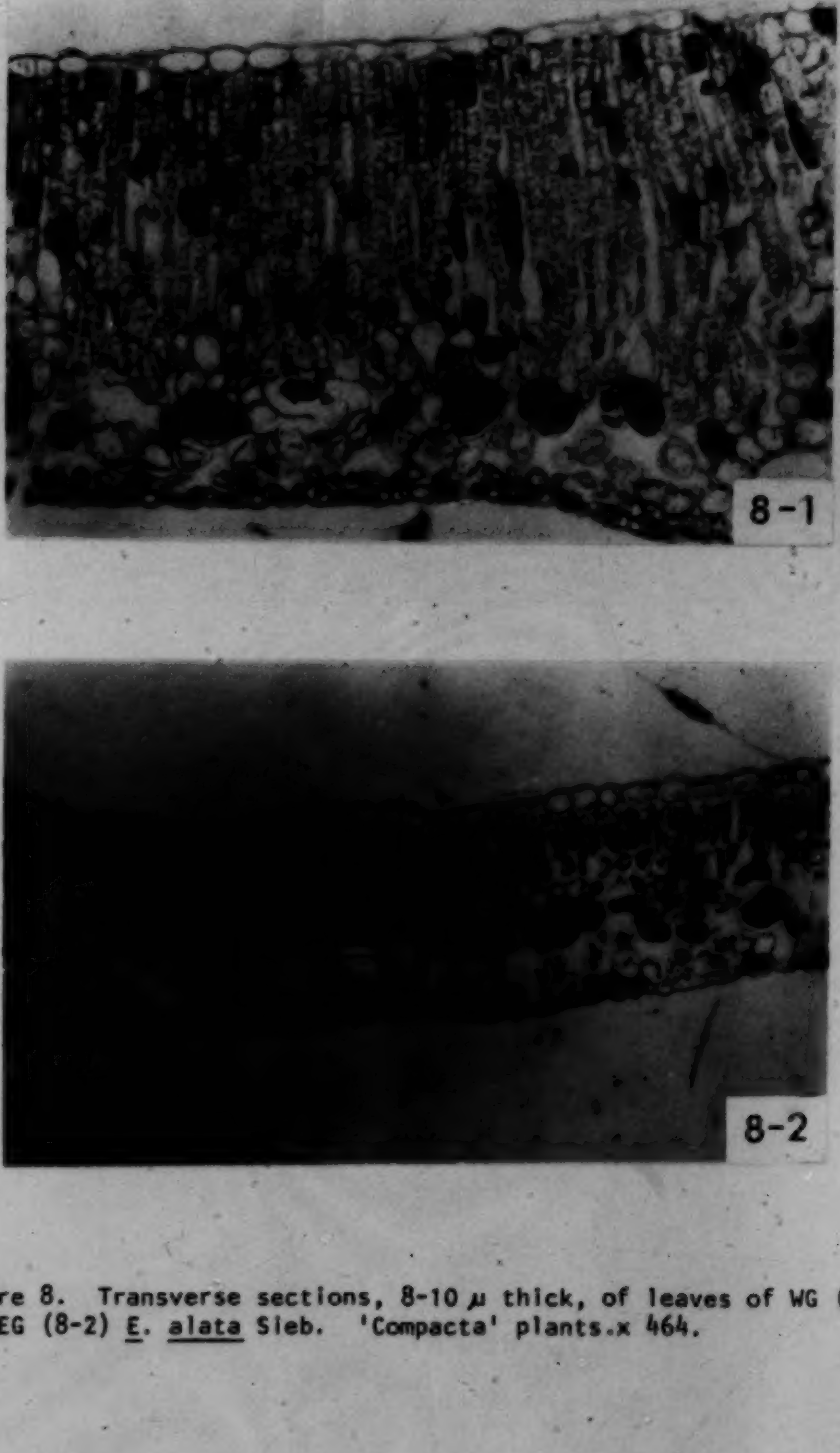


Figure 8. Transverse sections, 8-10 µ thick, of leaves of WG (8-1) and EG (8-2) *E. alata* Sieb. 'Compacta' plants.x 464.

and Kozlowski 1960]. Comparisons of total solar radiation throughout the growing season in Edmonton and in Ottawa and Toronto indicate that total solar radiation is signficantly greater in Western Canada only for the month of May and not later in the season when terminal and lateral buds are formed. Differences in light intensity could therefore be expected to have had little effect on morphology of the leaves of the field plants examined in this study.

The possibility of light intensity effecting the anatomical differences observed in the EG and WG leaves cannot, however, be completely discounted. The unit of measurement used for total solar radiation, the Langely, is a meteorological one representing the total amount of energy in the range of 300-3000 nm. Measurements of total energy do not relate well to plant growth because a large portion of the radiation is beyond the range of photosynthetic and photomorphogenic systems (Downs and Hellmers 1975). A comparison of energy levels in a specific segment of the electromagnetic spectrum in both Eastern and Western Canada, such as 400-700 nm (PAR), or at specific wavelengths, could however explain the observed anatomical differences in leaves of both plant types. Although specific radiation data of this nature is not available, a few general observations of differences in solar radiation at various geographical locations have been made. For example, Robertson (1966) noted that the far-red:red light ratio for a given season and solar elevation below 9°, was greater at higher latitudes than at lower latitudes. The amount of far-red and red light received at day-end has also been found to have substantial effects on plant growth (Downs et al 1958, Downs 1959, Kasperbauer et al 1970, Tso et al 1970, Tucker and Mansfield 1972, Sanchez and Cogliatti 1975), although detailed studies of the effect on leaf anatomy have not been reported.

A. Temperature and Photoperiod

The observed differences in anatomy of leaves of plants from Eastern and Western Canada and the leaves of EG and WG plants used in this study are likely partially due to temperatures and photoperiods occurring during leaf bud development and leaf expansion..

Leaves formed under Western temperatures and photoperiod (20°C/7°C, 18 hours) were larger and thicker than leaves formed under Eastern temperatures and photoperiod (23°C/13°C, 16 hours). This can be seen by comparing Treatments 2 and 4 in Table 9. Figure 9 shows that the leaves formed under Western conditions were thicker due to a larger amount of palisade parenchymatous tissue. The absolute thickness of spongy parenchymatous tissue did not change greatly between treatments.

The greater thickness of leaves formed under simulated Western conditions (20°C/7°C, 18 hour photoperiod) can be attributed more to the longer photoperiod rather than the cooler temperatures, (Table 9). When photoperiod was held at 16 hours, the thickness of leaves formed at 20°C/7°C (Treatment 1) was not significantly different from that of leaves formed at 23°C/13°C (Treatment 2). However, when temperature was held at 20°C/7°C, the thickness of leaves formed under an 18 hour photoperiod (Treatment 4) was significantly greater than the thickness of leaves formed under a 16 hour photoperiod (Treatment 1).

Even though the thickness of leaves formed under the cooler temperatures, 20°C/7°C, was not significantly different from that of leaves formed under the warmer temperatures, 23°C/13°C, it is worthwhile noting that there was a tendency shown towards greater thickness.

Table 9. Thickness of mature E. alata Sieb.'Compacta' leaves formed under various combinations of temperature and photoperiod.

Treatment No.	Condition Simulated	Mean Leaf thickness⁺ (mm)	Standard deviation (mm)
1	Western temperatures (20°C/7°C) Eastern photoperiod (16 hours) (PAR-420 $\mu E\ m^{-2}s^{-1}$	0.0186 a	0.0021
2	Eastern temperatures (23°C/13°C) Eastern photoperiod (16 hours) (PAR-420 $\mu E\ m^{-2}s^{-1}$)	0.0174 a	0.0031
3	Western temperatures (20°C/7°C) Eastern photoperiod (16 hours) (PAR-380 $\mu E\ m^{-2}s^{-1}$)	0.0176 a	0.0024
4	Western temperatures (20°C/7°C) Western photoperiod (18 hours) (PAR-380 $\mu E\ m^{-2}s^{-1}$)	0.0221 b	0.0042

+ Mean values, when not followed by a letter in common, are significantly different according to the Duncan's multiple range test ($p=0.05$).

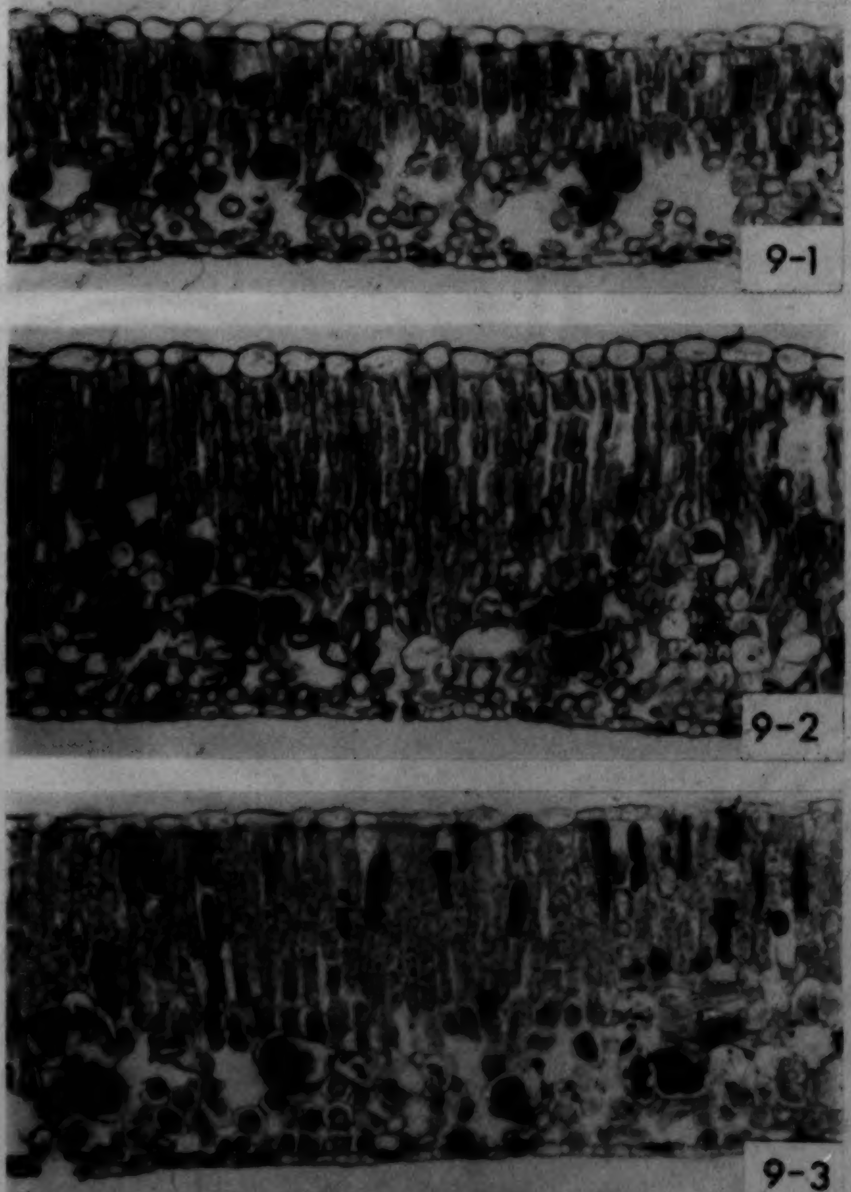


Figure 9. Transverse sections, 8-10μ thick, of leaves of EG *E. alata* Sieb. 'Compacta' plants formed under (9-1) simulated Eastern conditions (23°C/13°C, 16 hour photoperiod), (9-2) simulated Western conditions (20°C/ 7°C, 18 hour photoperiod) and (9-3) 20°C/7°C and a 16 hour photoperiod. x 464.

A comparison of Treatments 1 and 3, Table 9, illustrates that the light intensity used in the longer photoperiod treatment, reduced from that used in the 16 hour photoperiod treatment in order to expose plants to same total quantity of light per day, did not produce a statistically significant difference in leaf thickness.

This observed effect of photoperiod on leaf thickness and anatomy concurs with the results of some studies reported in the literature but not with others. It is likely due to the fact that the effect of photoperiod on leaf anatomy appears to be largely species dependent. The effect of photoperiod on leaf anatomy observed in this study is consistent with that observed by Margaris and Papadopoulou (1975) in Mongolian Cherry, Prunus fruticosa. These workers reported that leaves formed under long days were xeromorphic in nature with an increased proportion of palisade to spongy parenchymatous tissue. Nitsch (1957) also noticed an increased thickness of leaves of Peach, Prunus persica under long days, however this was due to an increased proportion of spongy parenchymatous tissue. On the other hand, the effect of long days on leaves of herbaceous plants appears to be quite different from that on woody plants. Vince-Prue (1975) reports that with most herbaceous plants studied, leaves formed under long days were thinner than those formed under shorter days.

The relatively thicker leaves of Euonymus formed in Western temperatures and in either an 18 or 16 hour photoperiod also appeared darker green than those formed in warmer temperatures and a 16 hour photoperiod. The darker color of the leaves, however, did not result from a higher total amount of chlorophyll. There was no significant difference in chlorophyll content between any of these three treatments (Table 10) when chlorophyll was expressed on an area basis. However, when chlorophyll content was expressed on a weight basis, it was shown to be inversely related to leaf thickness. A comparison of these two methods of expressing chlorophyll content implies that the darker green pigmentation of the thicker leaves must therefore have been due to a difference in distribution of chlorophyll, that is, over a greater depth of palisade parenchyma cells. A comparison of Treatments 1 and 3 in Table 10 indicates that light intensity had no independent influence on leaf chlorophyll.

From observations of controlled environment treatments on leaf morphology and anatomy it is apparent that differences in photoperiod and temperature are the factors contributing to the marked difference in leaves of plants growing in these two regions. If photoperiod and temperature influenced development of leaf primordia during bud formation, in a manner similar to the way leaf expansion was affected then regional differences in these two environmental parameters could also explain morphological and anatomical differences noted in the leaves of EG and WG plants. This possibility exists because treatments simulating Eastern and Western growing conditions during leaf expansion and maturation (June-July) are the same growing conditions that occur at the time of bud formation and differentiation of leaf primordia. There is some evidence that environment during bud formation plays a role in determining morphology and anatomy of shoots produced the next season (Haberlandt 1914, Kramer and Kozlowski 1960). Mikola (1962), for example, concluded that annual extension growth of Scotch pine, *Pinus sylvestris*, was determined mainly by temperature of the preceding

Table 10. Chlorophyll content in leaves *E. alata* Sieb 'Compacta' formed under Eastern and Western temperatures and photoperiods.

Treatment No.	Condition simulated	Chlorophyll Content+					
		Chlorophyll a		Chlorophyll b		Total chlorophyll	
		mg cm^{-2}	mg g^{-1}	mg cm^{-2}	mg g^{-1}	mg cm^{-2}	mg g^{-1}
1	Western temperatures (20°C/7°C) Eastern photoperiod (16 hours) (PAR-420 $\mu E\ m^{-2}s^{-1}$)	0.057 a	3.7 b	0.017 a	1.3 b	0.075 a	4.9 b
2	Eastern temperatures (23°C/13°C) Eastern photoperiod (16 hours) (PAR-420 $\mu E\ m^{-2}s^{-1}$)	0.050 a	4.6 a	0.020 a	2.0 a	0.072 a	6.1 a
3	Western temperatures (20°C/7°C) Eastern photoperiod (16 hours) (PAR-380 $\mu E\ m^{-2}s^{-1}$)	0.055 a	3.5 b	0.020 a	1.2 b	0.074 a	4.8 b
4	Western temperatures (20°C/7°C) Western photoperiod (18 hours) (PAR-320 $\mu E\ m^{-2}s^{-1}$)	0.053 a	2.4 c	0.021 a	0.9 b	0.075 a	3.5 c

+ Mean values in each column, when not followed by a letter in common are significantly different according to Duncan's multiple range test ($p=0.05$).

season. Also, Muelder and Schaeffer (1962) observed shoot growth on Western Yellow Pine, Pinus ponderosa in California to be closely related to June-July precipitation of the previous year.

As well as affecting leaf morphology, the photoperiod treatments conducted under controlled environment conditions, also influenced the initiation of lammas shoots (those resulting from breaking the dormancy of a current-year terminal bud). When temperature was held at 20°C/7°C, approximately 11 lammas shoots were formed under the 18 hour (Western) photoperiod treatment whereas 40 were formed under the the 16 hour (Eastern) photoperiod treatment. Production of lammas shoots is a commonly observed phenomenon in some species. For example, bud dormancy of Fagus seedlings can be broken at anytime by continuous light (Kozlowski 1971). In other genera, such as pine, Pinus (Wareing 1956) and Oak, Quercus species (Kozlowski 1971), dormancy can be broken by long days, but only if the buds are in a relatively mild state of dormancy.

II. Effects of Environment on Senescence Phenomena

A. Temperature

1. Field Experiments

The maximum daily temperatures to which EG Euonymus field plants were exposed from September 17, to November 8, 1976 are shown in Figure 10-1. The modified and noncontrolled minimum temperatures during this same period are shown in Figure 10-2. Although the heaters and covers used to provide the modified field condition did not maintain the desired 5°C, minimum temperatures nevertheless closely approximated those of Eastern Canada.

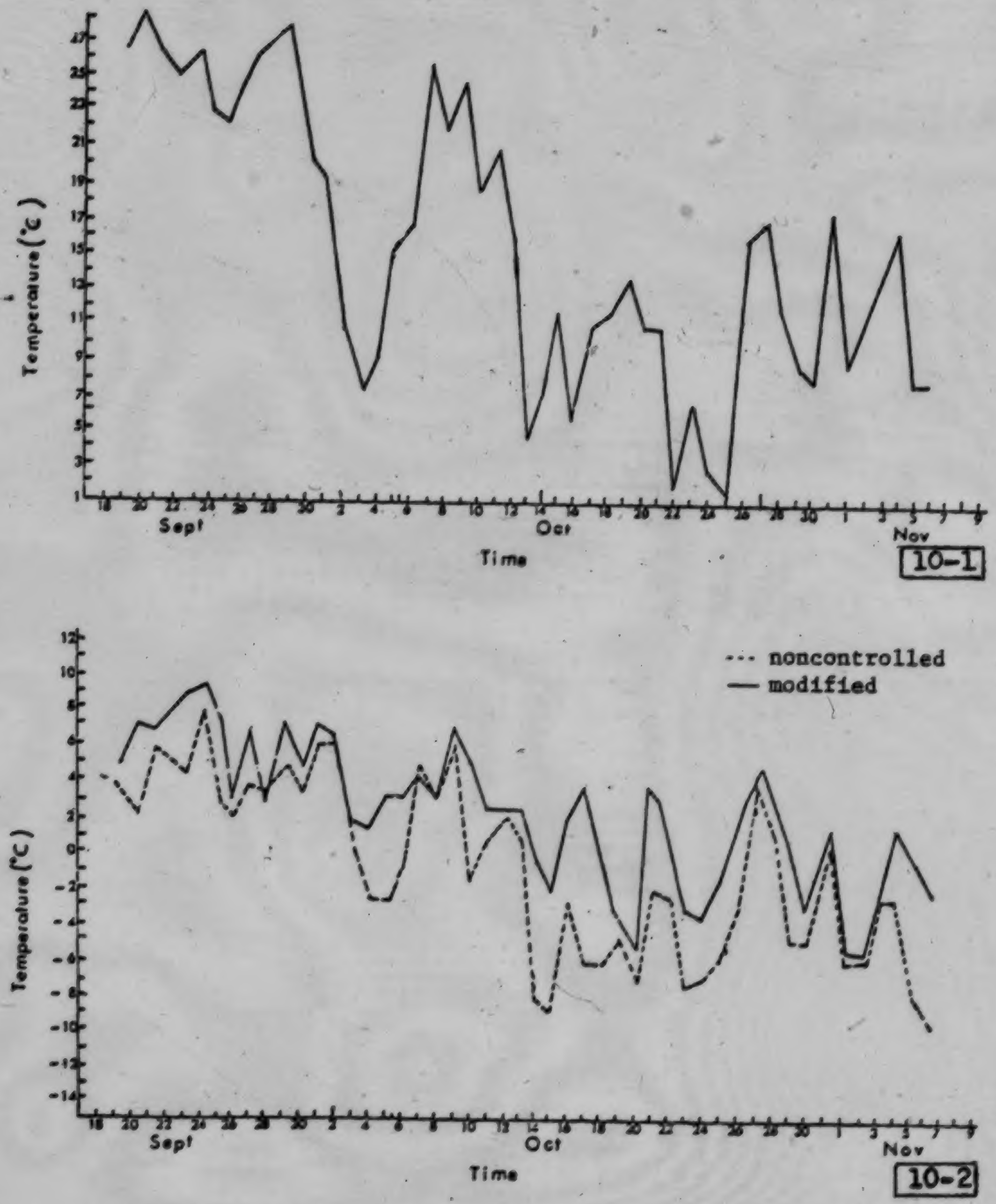


Figure 10. Maximum (10-1) and modified and noncontrolled minimum (10-2) field temperatures to which EG *E. alata* Sieb. 'Compacta' were exposed, September 17 to November 8, 1976.

From visual observation it was noted that the modified field temperature allowed greater development of autumn coloration than the noncontrolled temperatures. As explained in the following paragraphs, this was because of greater chlorophyll degradation rather than an increased accumulation of anthocyanins.

The effect on chlorophyll degradation of the minimum temperature encountered in the modified field treatment may be seen in Figure 11. Chlorophyll degradation started about October 6, 1976 and declined steadily. The lowest concentration was reached just prior to leaf abscission on November 8, 1976. Total chlorophyll, chlorophyll a and chlorophyll b content decreased 89.1%, 85.9% and 85.6% respectively, over the test period.

Total chlorophyll in leaves of plants exposed to noncontrolled temperatures did not decline steadily but did so in stages. There was a statistically significant drop in total chlorophyll on two occasions during leaf senescence; the first starting October 6 and the second, October 27. Total chlorophyll content did not alter significantly between October 14 and 27 and between October 28 and November 8. The decline in total chlorophyll, chlorophyll a and chlorophyll b was significantly smaller during the period of observation than in plants exposed to the modified temperature with only 47.4%, 52.6% and 32.1% respectively, of the initial content being degraded.

The pattern of chlorophyll degradation in response to both treatments can be related to the daily changes in temperature to which the plants were exposed. The drop in temperature on October 4 and 5 appeared to trigger chlorophyll degradation in both treatments.

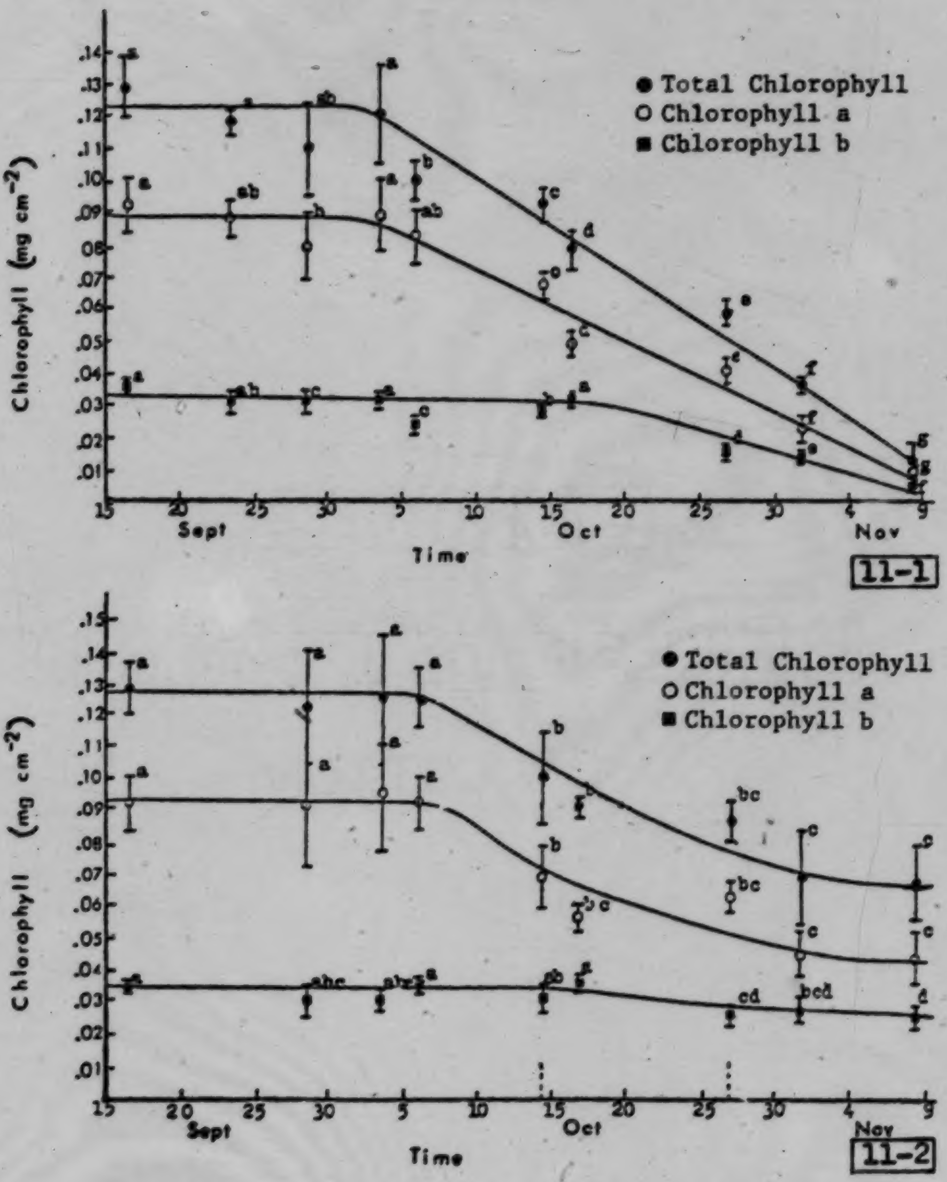


Figure ~~11.~~ Decline in chlorophyll content[1] of leaves of EG *E. alata* Sieb. 'Compacta' exposed to modified (11-1) and noncontrolled (11-2) field temperatures from September 17 to November 8, 1976.[1]

[1] Mean values used to plot each curve when not followed by a letter in common are significantly different according to Duncan's multiple range test ($p=0.05$). Bars associated with mean values indicate standard error of mean.

From September 17 to October 2 the average minimum temperature in the two treatments was 6.4°C and 4.1°C, respectively. The lowest temperature reached on October 4 in the modified temperature treatment was 2.0°C and in the noncontrolled, -2.0°C.

Mild temperatures between October 6 and 13 appeared to promote chlorophyll degradation with the result that similar concentrations of chlorophyll were noted in leaves of plants from both treatments on October 14. Average minimum temperature during this period was 3.9°C in the modified temperature treatment and 2.1°C in the noncontrolled temperature treatment.

Chlorophyll degradation was slowed in the noncontrolled temperature treatment on October 14 by a minimum temperature of -7.8°C. As a result of this sudden drop in temperature and a subsequent average minimum daily temperature of -4.3°C, there was little further chlorophyll degradation in these plants. During the same period a temperature drop to 0.0°C on October 14 and a subsequent average daily minimum temperature of 1.3°C did not affect chlorophyll degradation in the modified treatment. The process continued in these plants right up to November 8 and changes in chlorophyll content were statistically significant.

Anthocyanin build-up, unlike chlorophyll degradation was not influenced by exposure to either of the two temperature regimes. Changes in anthocyanin content over the period of observation for the noncontrolled and modified temperature treatments are shown in Figure 12.

The maximum concentrations of anthocyanin reached in the modified and noncontrolled temperature treatments, (respectively,

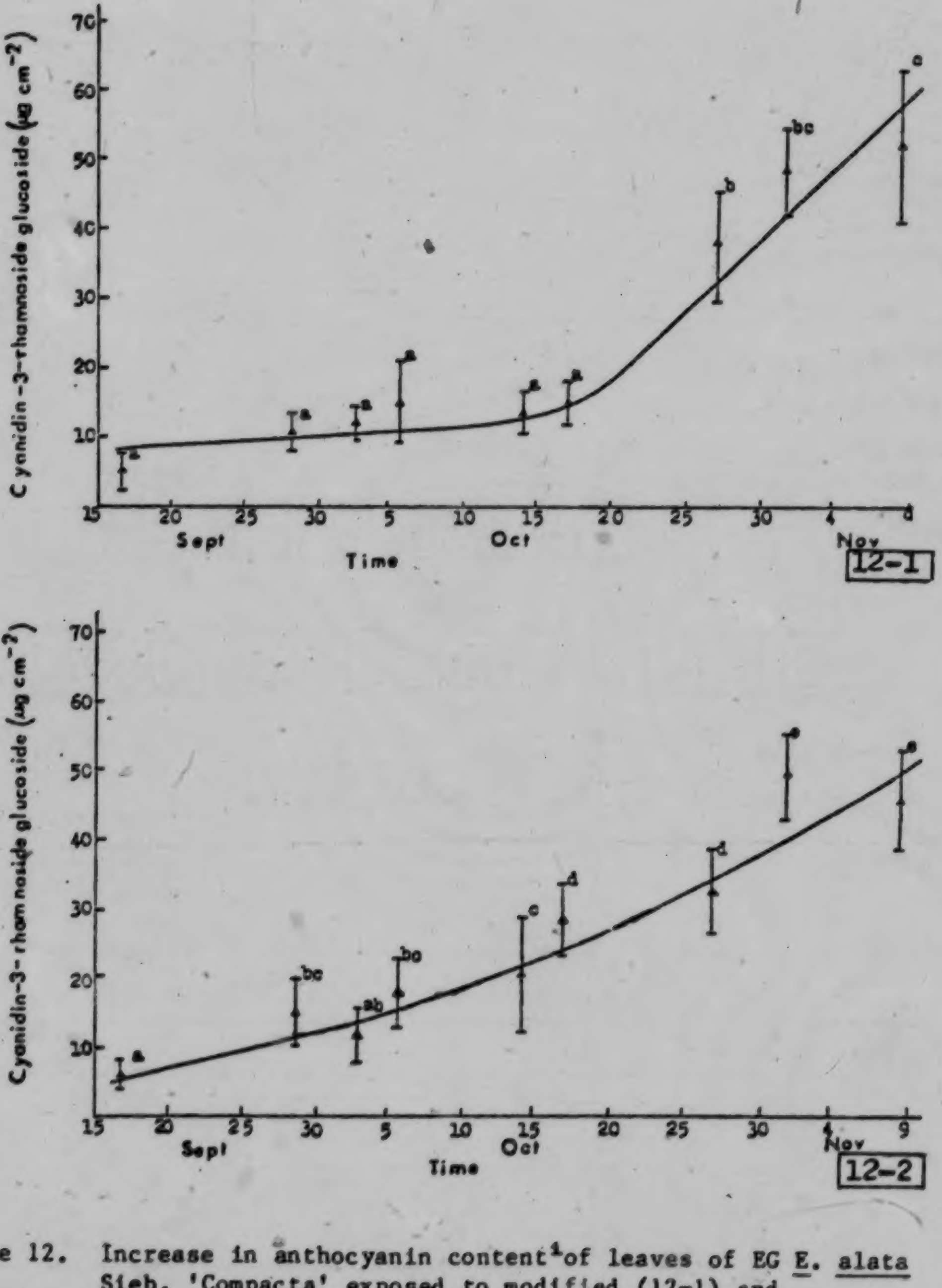


Figure 12. Increase in anthocyanin content[1] of leaves of EG E. alata Sieb. 'Compacta' exposed to modified (12-1) and noncontrolled (12-2) field temperatures from September 17 to November 8, 1976.[1]

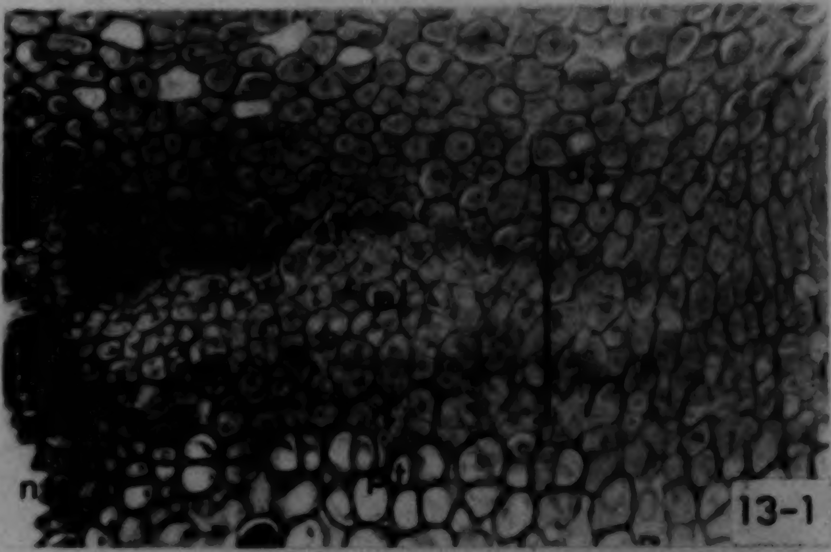
[1] Mean values used to plot each curve when not followed by a letter in common are significantly different according to Duncan's multiple range test ($p=0.05$). Bars associated with mean values indicate standard error of mean.

52.3629 ± 11.0722 µg cy-3-rh glu cm^{-2} and 46.2501 ± 7.1509 µg cy-3-rh glu cm^{-2} leaf tissue) were not statistically different from one another. Anthocyanin accumulation, however was initiated at different times in the two treatments. In the modified treatment, anthocyanin levels did not increase significantly until October 17, whereas in plants from the noncontrolled treatment such increases started right from the beginning of the test period.

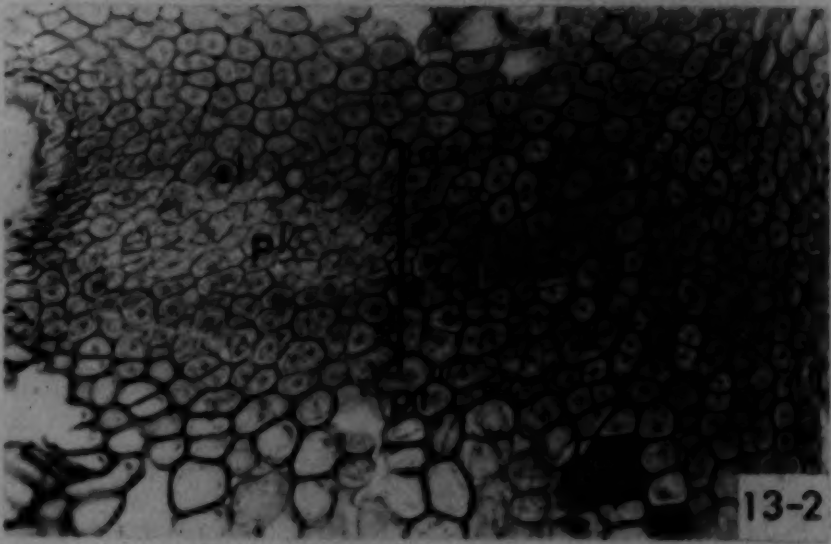
Daily changes in temperature during the test period (see Figure 10) also account for the observed trends in anthocyanin accumulation in the two treatments. In the noncontrolled temperature treatment, anthocyanin content changed in stages as did chlorophyll content. In the modified treatment, anthocyanin content increased steadily and gradually over time just as chlorophyll content decreased steadily and gradually over time.

The process of leaf abscission in Euonymus during senescence, was also shown to be sensitive to temperature. More leaves remained on the plants in the noncontrolled temperature treatment on November 8, 1976 (end of the sampling period) than on plants in the modified temperature treatment. It was also more difficult to manually remove leaves from plants in the noncontrolled treatment than from plants in the modified treatment. The larger number of leaves remaining on plants in the noncontrolled temperature treatment could be due to cold induced damage to cells of the abscission zone. Addicott (1968) states that low temperature damage of this nature can completely prevent biochemical changes necessary to induce leaf abscission.

The abscission zones of leaves from both the modified and noncontrolled temperature treatments, are shown in Figure 13. These



13-1



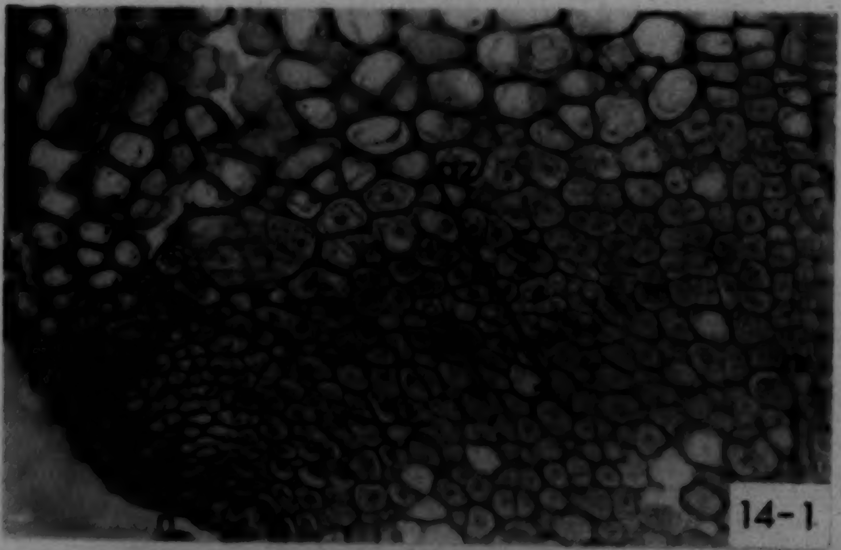
13-2

Figure 13. Longitudinal sections, 8-10 μ thick, of the abscission zone of leaves of EG *E. alata* Sieb. 'Compacta' plants exposed to modified (13-1) and non-controlled (13-2) field temperatures, November 1, 1976. x 763.
az - abscission zone, n - notch, external indicator of az, pl - protective layer, pt - petiole tissue, sl - separation layer.

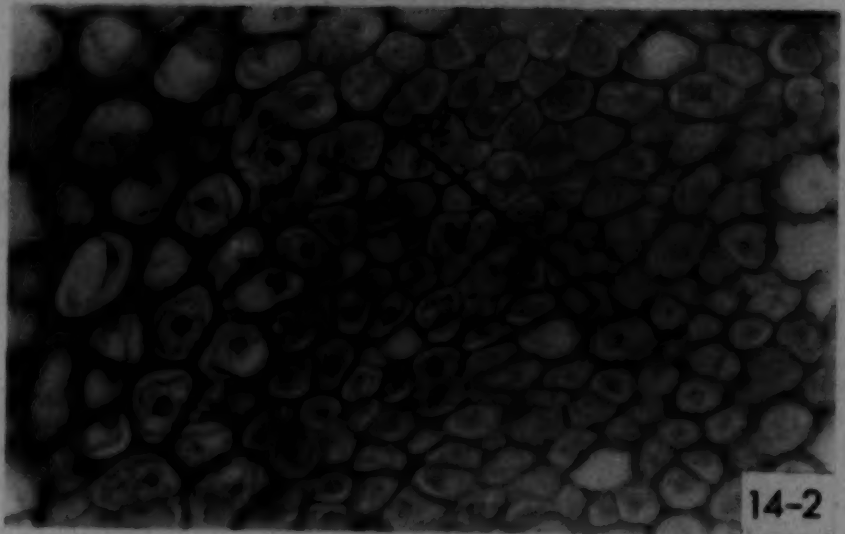
are to be compared with Figures 14 and 15 which show, respectively, the abscission zone of leaves of nonsenescing EG potted plants and of leaves from EG potted plants which were more highly colored than those from both field temperature treatments.

The abscission zone of the nonsenescing EG potted plants was not well developed (see Figure 14). The band of cell divisions delineating the zone, was relatively narrow, 7-9 cells wide, whereas a completely developed abscission zone is approximately 12-16 cells wide (Facey 1950). In some sections examined, division had started in the outer cortical layers but had not progressed inwards to span the entire abscission zone. Webster (1970) working with Red kidney bean, Phaseolus vulgaris 'Red Kidney' and Facey (1950) working with American Ash, Fraxinus americana, noted that cell division proceeded with time from the outer to the inner cortical layers. The abscission zone of the nonsenescing EG plants did not appear lighter in color than the surrounding tissue. This was due to the absence of differential staining properties of the cell walls. Moline and Bostrak (1972) state that differential cell wall staining is indicative of advanced development in the abscission zone. Also few cell walls in the abscission zone had thickened, and this, according to Fahn (1973), is another sign of an immature abscission zone.

On the other hand, the abscission zone of the highly colored leaves of Euonymus was in a very advanced state of anatomical development (see Figure 15). Extensive cell division within the zone had resulted in it reaching a width of approximately 16 cells. The zone, for the most part, was lightly stained and walls of most cells in were thick. Cell division was also apparent in the leaf traces,



14-1



14-2

Figure 14. Longitudinal sections, 8-10 μ thick, of the abscission zone of non-senescing leaves of EG E. alata Sieb. 'Compacta' potted plants. x 763 (14-1) and x 1160 (14-2).

az - abscission zone, n - notch, external indicator of az

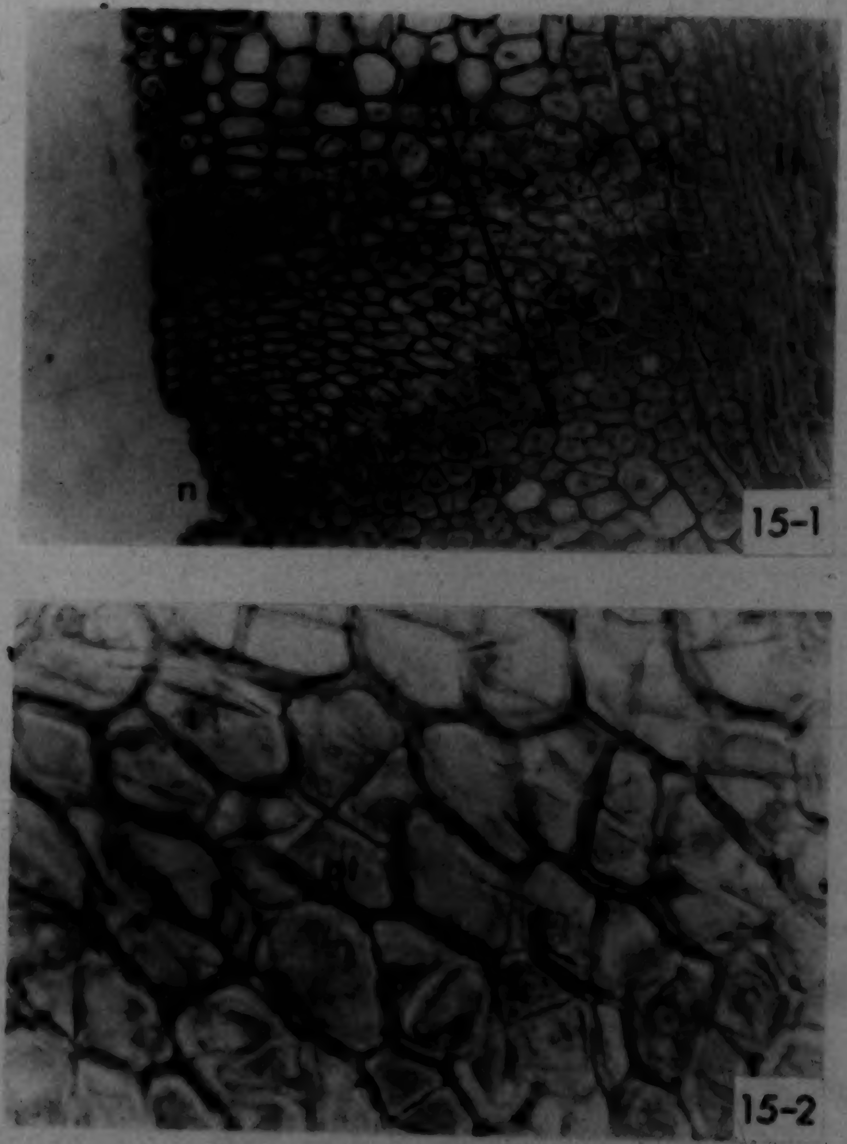


Figure 15. Longitudinal sections, 8-10 μ thick, of the abscission zone of highly colored senescing leaves just prior to their abscission from EG E. alata Sieb. 'Compacta' potted plants. x 763 (15-1), x 2925 (15-2).

az - abscission zone, lt - leaf traces, n - notch, external indicator of az, pl - protective layer, pt - petiole tissue, sl - separation layer.

which according to Facey (1950), was another sign of advanced maturity of the abscission zone.

Based on anatomical investigation, the development of the abcission zones in leaves from both field temperature treatments (Figure 13) was intermediate to those of the two other sample types studied. The abscission zones of leaves from both field treatments were more darkly stained than those of the highly colored senescing leaves but more lightly stained than those of nonsenescing leaves of EG plants. Also, the zones from the two field treatments were both approximately 11-13 cells wide compared to 7-9 cells wide in the nonsenescing leaves, and to 16 cells wide in samples taken from highly colored senescing leaves of EG plants.

Little difference in anatomical development of the abscission zones of leaves from the two field treatments was noted. The difference in the amount of force which was required to manually remove leaves from these plants must therefore be explained by the effect of temperature on chemical changes occurring within cell walls to effect abscission.

Field temperatures did not effect changes in α-amino nitrogen content as they did with other senescence processes studied (see Figure 16). Concentration of α- amino nitrogen was initially 0.264 and 0.632 μg alanine cm^{-2} leaf tissue in the noncontrolled and modified temperature treatments respectively. Concentrations began to increase about October 15, ten days after the start of chlorophyll degradation but there was little difference in the final concentrations noted in the two treatments.

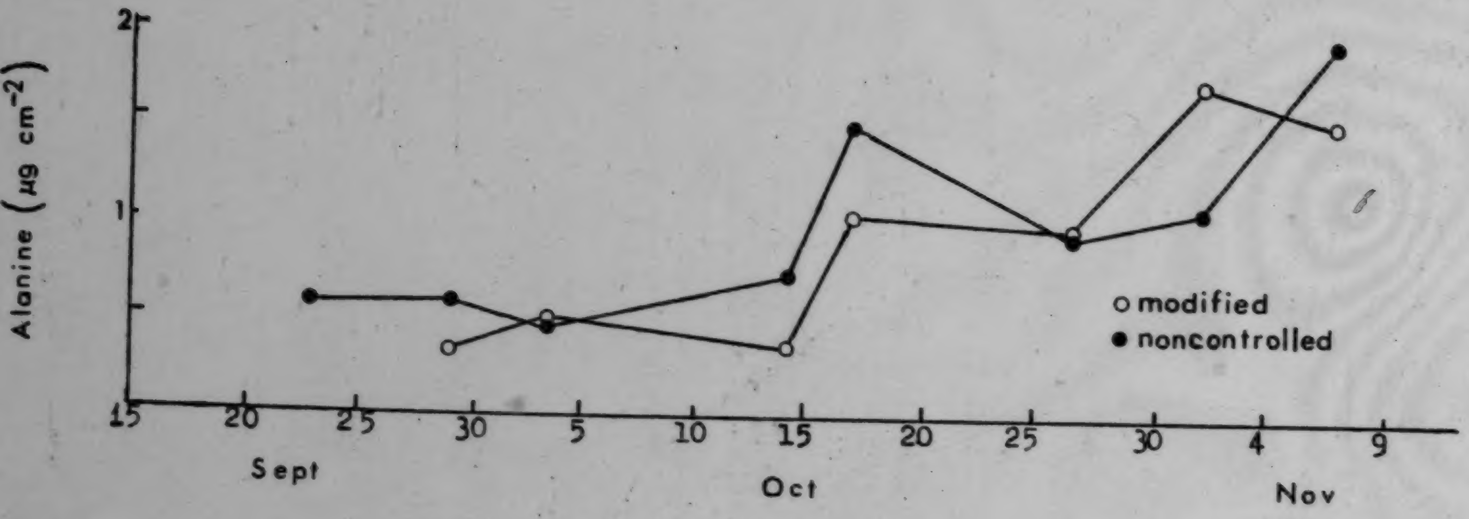


Figure 16. Concentration of α-amino nitrogen in leaves of EG *E. alata* Sieb. 'Compacta' in the modified and noncontrolled field temperature treatments, September 22 to November 8, 1976.

The apparent lack of effect of temperature on α-amino nitrogen content of tissues in which the degree of chlorophyll degradation differs, are consistent with observations made by Osborne (1973). She states that under conditions of stress, where chlorophyll is not completely degraded, certain processes like photosynthesis and protein change, may be reduced to levels noted in senescent tissue where chlorophyll has been fully degraded.

The observed changes in α-amino nitrogen with time in both treatments, are similar to those noted by other researchers working with senescent tissue. Yemm (1937, 1950) found α-amino nitrogen in bean leaves, Phaseolus vulgaris to increase steadily as the time lengthened between removal and analysis of leaves. Plaisted (1958b) noted in Norway Maple, Acer platanoides that soluble nitrogen compounds began to increase in concentration 30 days before leaf abscission. This is approximately the same time that the increase in soluble nitrogen in leaves of E. alata Sieb. 'Compacta' occurred.

The source of the observed increase in α-amino nitrogen in leaves of E. alata Sieb. 'Compacta' plants is not obvious from this study. It is not very likely that the increase arose from proteolysis of chloroplast protein as suggested to be the case by Plaisted (1958b) in Norway Maple, Acer platanoides, or by Lewington (1967) in cucumber, Cucumis sativum. If the increase in α-amino nitrogen did arise from this source, the greater concentration would have been expected in the modified temperature treatment because of the more extensive degradation of chlorophyll. There was also too long an interval (10 days) between the beginning of chlorophyll degradation and the beginning of the increase in α-amino nitrogen content for the proteolysis of chloroplast proteins to have produced the observed results. The increase however, could have resulted, from proteolysis of other proteins.

2. Controlled Environment Experiments

The temperature treatments to which plants were exposed under controlled environment conditions, affected chlorophyll degradation and anthocyanin accumulation in a manner similar to that observed in the field. Steady, non-freezing temperatures (15°C/2°C and 15°C/5°C), that occurred at intervals in the modified temperature field treatment, promoted rapid senescent pigment changes. On the other hand, sudden drops in temperature to sub-freezing levels (15°C/0°C/-5°C) as occurred in the noncontrolled temperature-field treatment, decreased the rate and the extent of pigment change.

In this experiment a 15°C/2°C temperature treatment, was used to simulate a temperature regime that would be roughly midway between those common to autumn temperatures of Eastern and Western Canada. The effect of this treatment on chlorophyll degradation is shown in Figure 17-1. Chlorophyll degradation was induced after approximately 23 days of treatment conditions. Chlorophyll concentration immediately prior to leaf abscission (47 days after the start of the treatment) was 0.0142 ± 0.0021 mg cm^{-2} leaf tissue, 14.6% of the initial value.

The effect of the 15°C/2°C temperature treatment on anthocyanin accumulation is shown in Figure 17-2. Anthocyanin concentration reached measurable levels just prior to rapid chlorophyll degradation and showed a linear increase over time, to reach a final concentration before leaf abscission of 33.1264 ± 2.0122 μg cy-3-rh glu cm^{-2} leaf tissue.

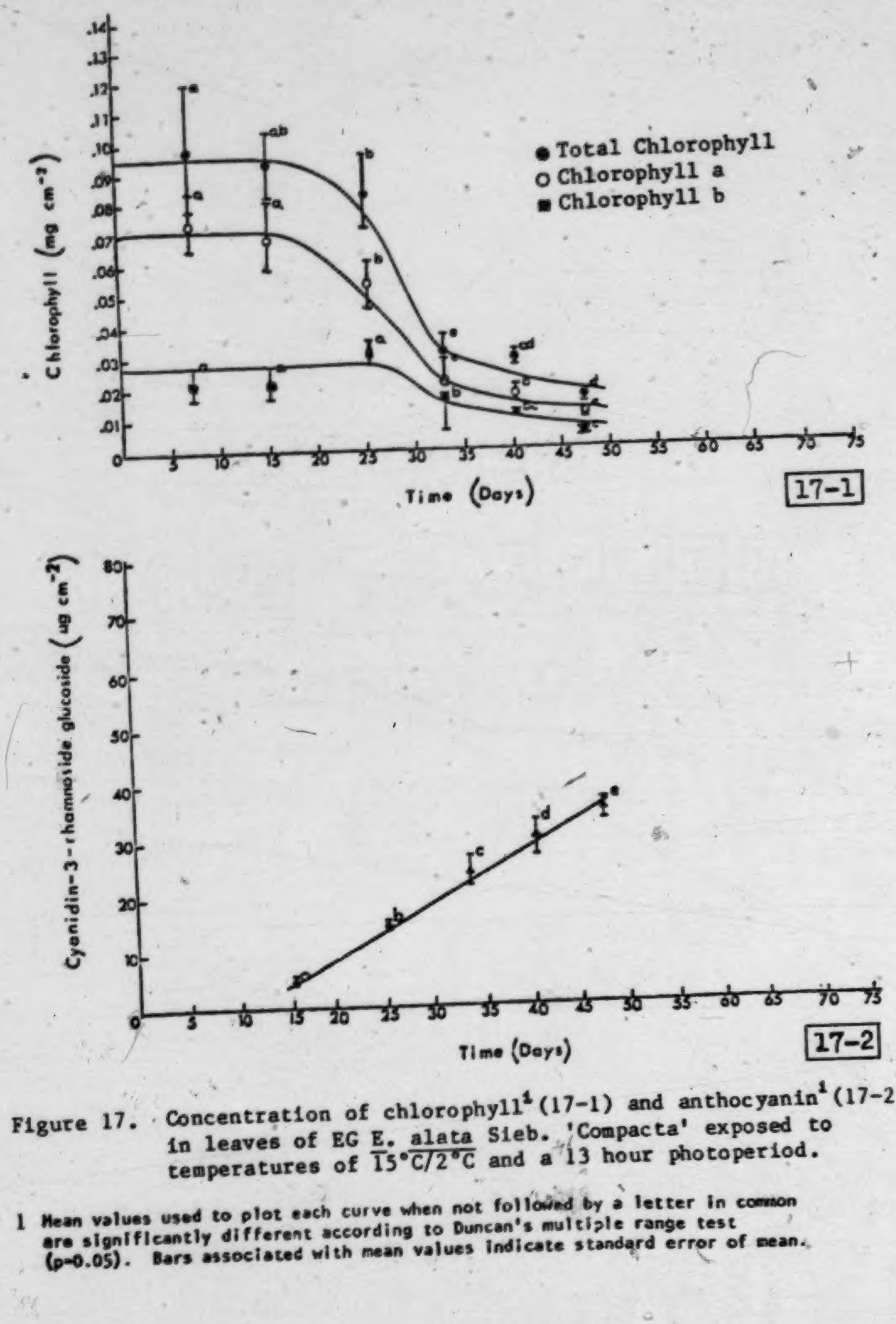


Figure 17. Concentration of chlorophyll[1] (17-1) and anthocyanin[1] (17-2) in leaves of EG E. alata Sieb. 'Compacta' exposed to temperatures of 15°C/2°C and a 13 hour photoperiod.

[1] Mean values used to plot each curve when not followed by a letter in common are significantly different according to Duncan's multiple range test (p=0.05). Bars associated with mean values indicate standard error of mean.

Creasy (1974) noted similar changes in pigments of E. alata in response to 15°C/2°C and a 10 hour day. Chlorophyll degradation in his experiments, however, occurred at a steady rate throughout the sampling period. This may have been due to the effect of the shorter day (10 hours) used in his experiments. In experiments reported here the length of day used was 13 hours.

The effect of the 15°C/5°C temperature treatment, used to simulate Eastern autumnal temperatures, on chlorophyll degradation and on anthocyanin accumulation is shown in Figures 18-1 and 18-2 respectively. As in the 15°C/2°C temperature treatment, chlorophyll levels began to drop sharply after 23 days of treatment. Final chlorophyll concentration was 0.0037 ± 0.0014 mg cm^{-2} leaf tissue before leaf abscission, 3.7% of its initial value. This value was significantly less than in the 15°C/2°C treatment. The slightly warmer night temperature of 5°C also allowed significantly more anthocyanin to accumulate than the cooler night temperature in the 15°C/2°C temperature treatment (51.0021 ± 2.1214 verses 33.1264 ± 2.0122 µg cy-3-rh glu cm^{-2} leaf tissue). From observations of these pigment changes, which resulted in plants with fully developed autumn color, it is likely that the 15°C/5°C treatment closely approximated Eastern autumnal temperatures.

Leaf coloration in the 15°C/5°C treatment, was also greater than in leaves of plants in the modified temperature-field treatment. This is undoubtedly due to the fact that, in the modified temperature treatment, minimum temperatures could not be fully controlled. The 15°C/2°C treatment, on the other hand, induced changes in chlorophyll content similar to those that occurred in the modified field

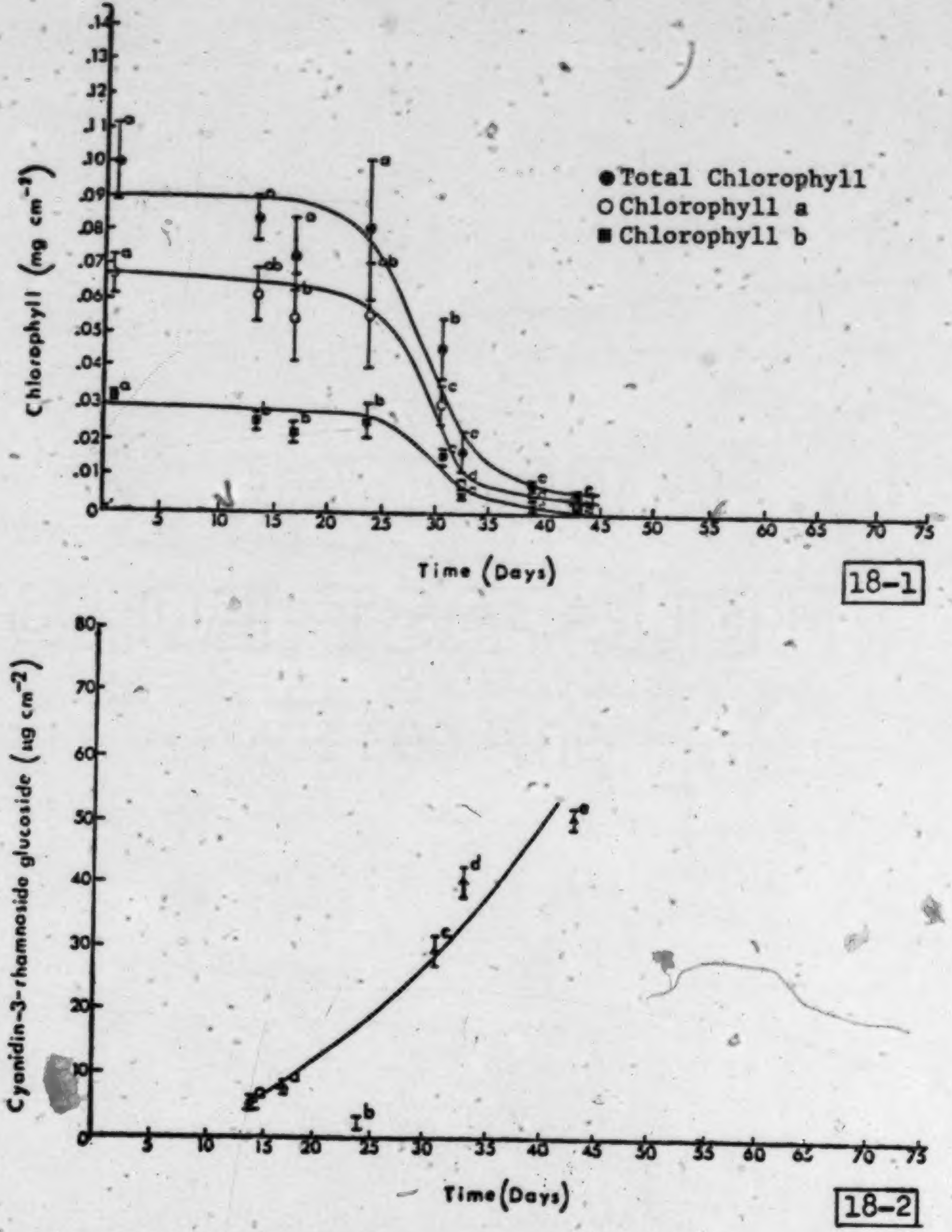


Figure 18. Concentration of chlorophyll[1] (18-1) and anthocyanin[1] (18-2) in leaves of EG *E. alata* Sieb. 'Compacta' exposed to simulated Eastern conditions (15°C/5°C, 13 hour photoperiod).

[1] Mean values used to plot each curve when not followed by a letter in common are significantly different according to Duncan's multiple range test ($p=0.05$). Bars associated with mean values indicate standard error of mean.

temperature-treatment. This is probably due to the fact that the temperatures encountered in these two treatments were very similar. Final chlorophyll concentration for the plants in the modified field temperature treatment was 0.0141 ± 0.0026 mg compared to 0.0142 ± 0.0021 mg cm^{-2} for those in the constant 15°C/2°C treatment.

Significantly less anthocyanin accumulated in leaves of plants in the 15°C/2°C temperature treatment than in leaves of plants in the modified field-temperature treatment (33.1264 ± 2.0122 versus 52.3629 ± 11.0722 µg cy-3-rh glu cm^{-2} leaf tissue). This may have been due to the lower light intensity of the controlled environment treatment. High light intensities have been known to cause higher concentrations of anthocyanin in senescing leaves (Creasy 1974, McClure 1975, Goodwin 1976).

It is not known whether the 15°C/5°C treatment provided temperatures optimum for leaf senescence and abscission in E. alata Sieb. 'Compacta' as only one other higher temperature treatment (18°C/10°C) was used. It should be noted, however, that leaf abscission took only 44 days in the 15°C/5°C treatment as opposed to 47 days in the 15°C/2°C treatment. From the results of the 18°C/10°C treatment it was clear that these temperatures were well above those optimum for leaf senescence of E. alata Sieb. 'Compacta'. No changes in chlorophyll content were noted after 39 days of treatment (see Figure 19) and leaves remained firmly attached to the plants.

The effect of the Western temperature treatment (15°C/2°C for 31 days and 15°C/0°C/-5°C for 19 days) on chlorophyll degradation is shown in Figure 20-1. As in all other controlled environment treatments, chlorophyll degradation started after approximately 23 days

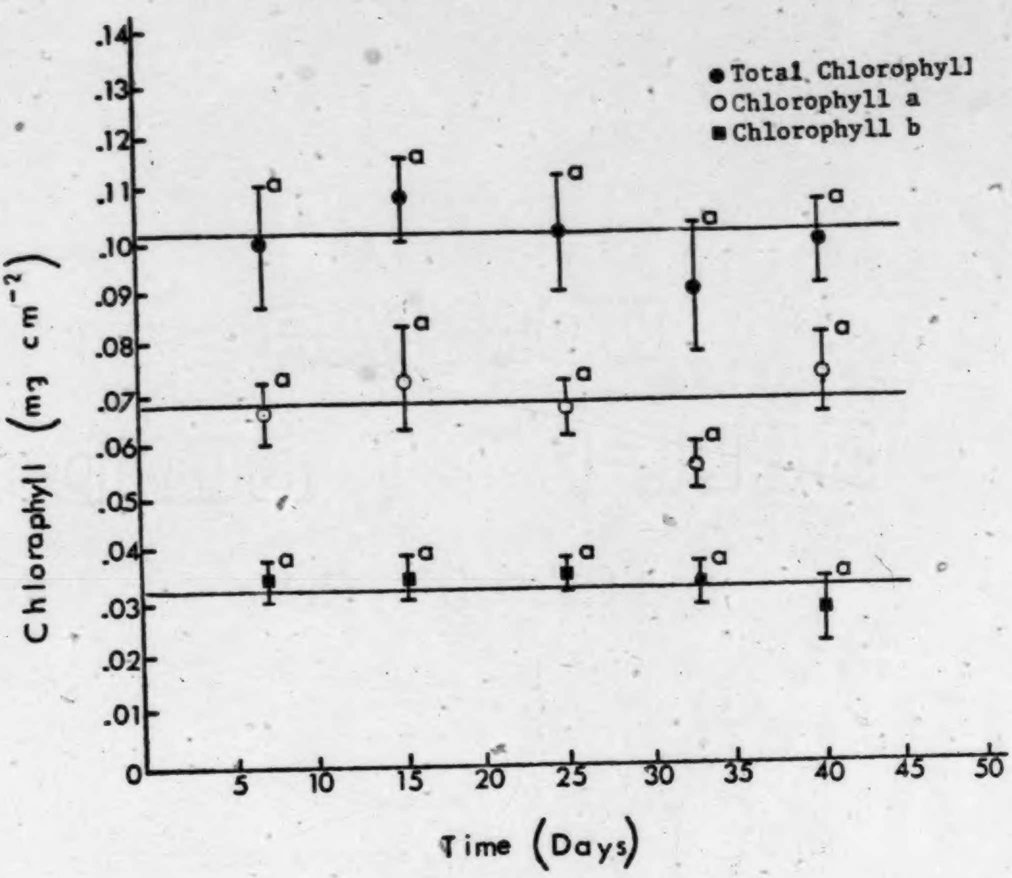


Figure 19. Concentration of chlorophyll[1] in leaves of EG *E. alata* Sieb. 'Compacta' exposed to temperatures of 18°C/10°C and a 13 hour photoperiod.

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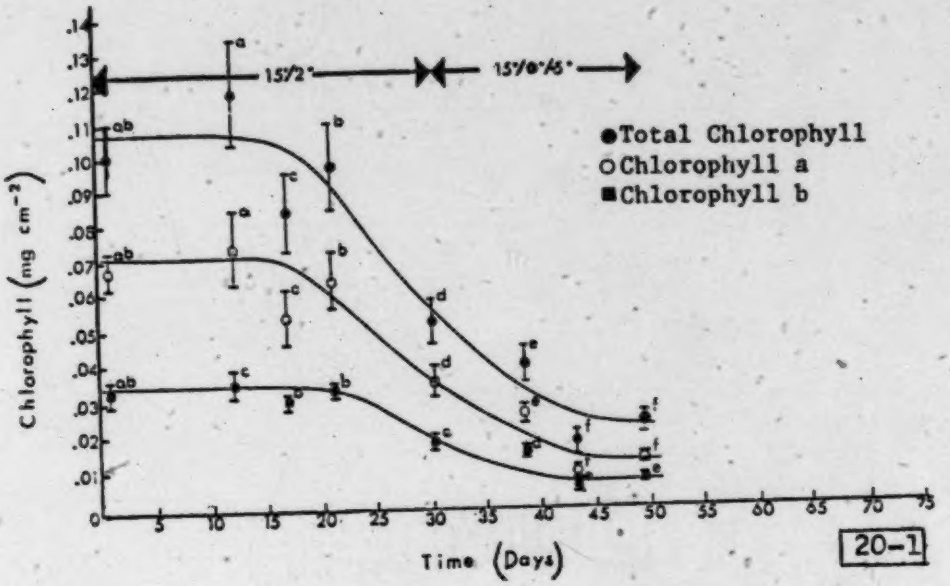
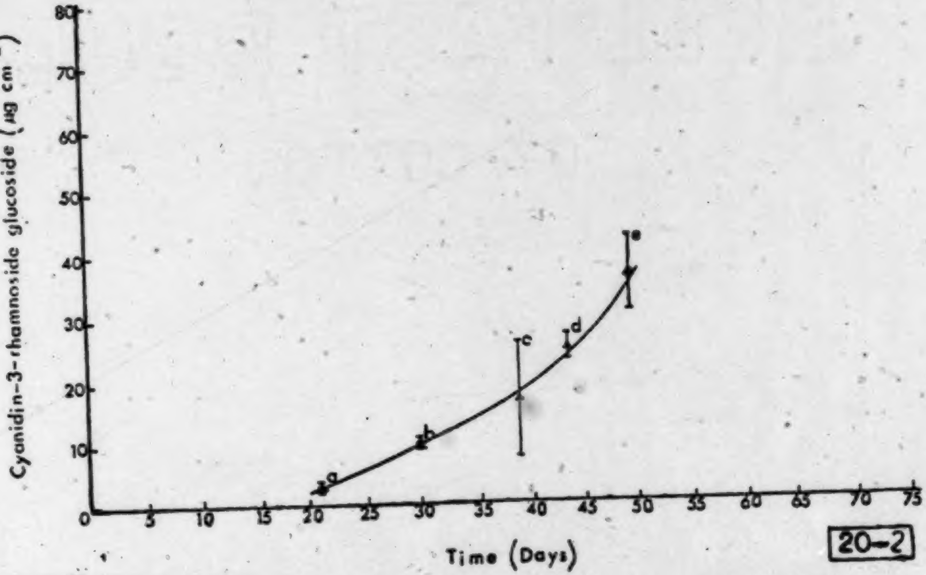
[1] Mean values used to plot each curve when not followed by a letter in common are significantly different according to Duncan's multiple range test ($p=0.05$). Bars associated with mean values indicate standard error of mean.



20-1



20-2

Figure 20. Concentration of chlorophyll[1](20-1) and anthocyanin[1](20-2) in leaves of EG *E. alata* Sieb. 'Compacta' exposed to simulated Western conditions (15°C/2°C, then 15°C/0°C/-5°C and a 13 hour photoperiod).

[1] Mean values used to plot each curve when not followed by a letter in common it on the are significantly different according to Duncan's multiple range test ($p = 0.05$). Bars associated with mean values indicate standard error of mean.

of treatment. However, a significantly higher concentration of chlorophyll remained in the leaves at the time of abscission than in the leaves of plants from the other temperature treatment. The final chlorophyll concentration in the 15°C/0°C/-5°C temperature treatment was 0.0206 ± 0.0018 mg chlorophyll cm^{-2} leaf tissue (20.8% of its initial value) compared to 0.0142 ± 0.0021 mg chlorophyll cm^{-2} leaf tissue (14.6% of its initial value) in the 15°C/2°C temperature treatment. This higher chlorophyll concentration resulted in the leaves appearing green at the time of abscission.

The effect of the 15°C/0°C/-5°C temperature treatment on anthocyanin content is shown in Figure 20-2. The lower minimum temperatures used here were no more effective in the accumulation of anthocyanin than were temperatures of 15°C/2°C. The maximum anthocyanin content reached was 36.5500 ± 6.5721 µg cy-3-rh glu cm^{-2} leaf tissue as compared to 33.1264 ± 2.0122 µg cy-3-rh cm^{-2} leaf tissue in the 15°C/2°C treatment.

The lower minimum temperature of the 15°C/0°C/-5°C treatment did however, affect leaf abscission. Leaves of plants in this treatment took longer to abscise than in both the other treatments.

The 15°C/0°C/-5°C and 15°C/2°C controlled environment treatments parallelled the effects of the two field treatments, but significantly more chlorophyll was degraded by the time of abscission in leaves of plants in the 15°C/0°C/-5°C controlled environment treatment. These results lend support to the hypothesis that autumn coloration of _E. alata_ Sieb. 'Compacta' is not promoted in Edmonton because sub-freezing temperatures prevent complete chlorophyll degradation.

B. Photoperiod

Photoperiod was found to have an effect on pigment changes and leaf abscission in Euonymus. Figure 21-1 and 21-2 show the effects on chlorophyll degradation of 13 and 18 hour treatments respectively, when temperatures were held at 15°C/2°C. Figure 22-1 and 22-2 show the effect of the same conditions on anthocyanin accumulation.

The longer day did not prevent the normal pigment changes associated with senescence, however it did delay their occurrence. When temperature was held at 15°C/2°C, it took 12 days longer in the 18 hour photoperiod to induce statistically significant changes in chlorophyll content. Under the same temperature conditions, changes in anthyocyanin content were also favored by the shorter day. Significant increases were noted 15 days earlier in the shorter photoperiod.

The fact that senescence was delayed (24 days) under the long day treatment is not unexpected. The fact that senescence occurred at all under long days supports the common observation that, in controlled environments, long days cannot delay senescence indefinitely when temperatures are low.

The degree of chlorophyll degradation was not influenced by the length of photoperiod treatment whereas the converse was true for anthocyanin accumulation. When plants were exposed to the 13 hour photoperiod, chlorophyll content just prior to abscission was 14.6% of the initial value. This was not significantly different from that of plants in the 18 hour photoperiod which was 14.1% of the initial value. However, significantly more anthoycanin accumulated in leaves of plants in the 18 hour photoperiod than in leaves of plants in the 13

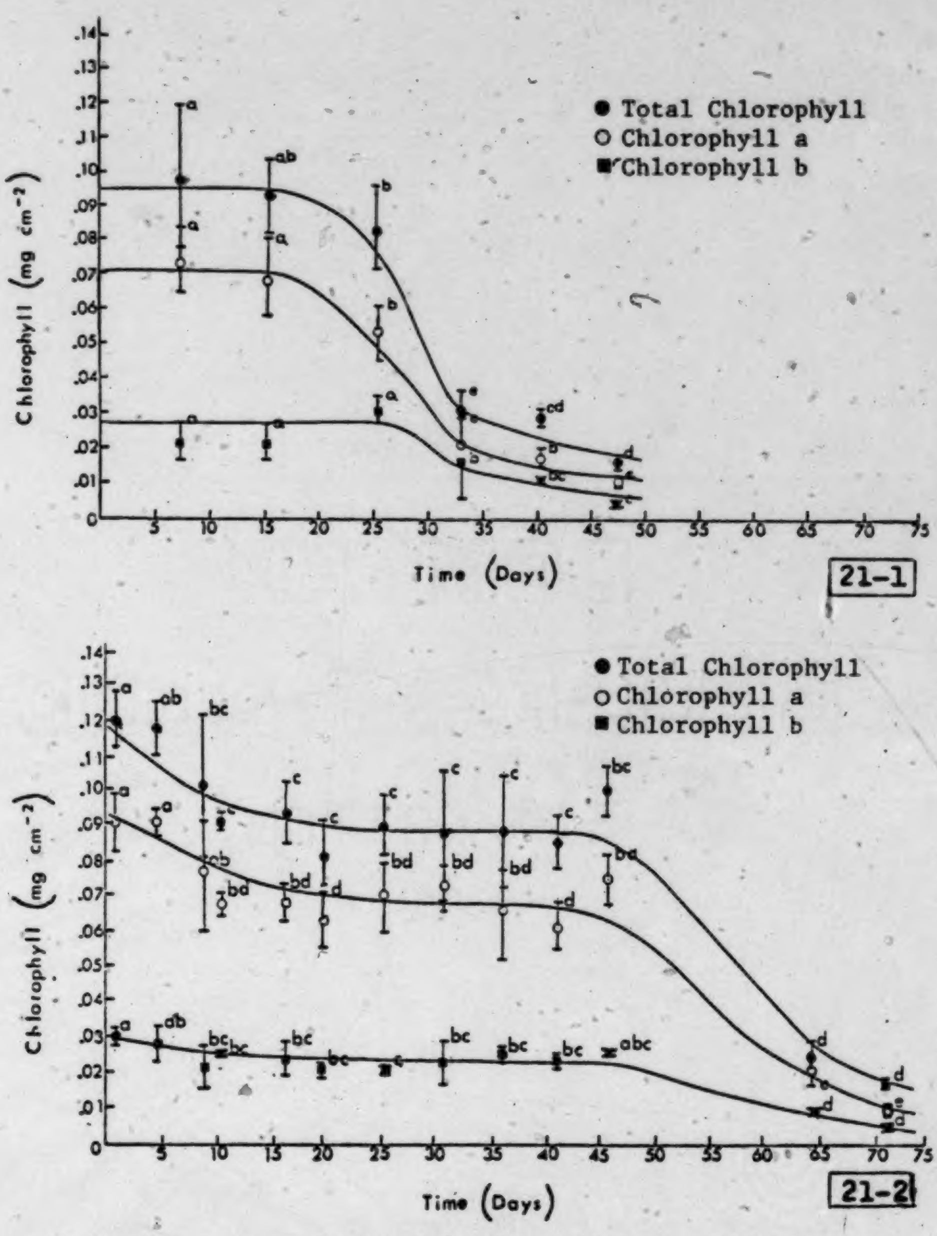


Figure 21. Decline in chlorophyll content[1] in leaves of EG E. alata Sieb. 'Compacta' exposed to temperatures of 15°C/2°C and a photoperiod of 13 hours (21-1) and 18 hours (21-2).

[1] Mean values used to plot each curve when not followed by a letter in common are significantly different according to Duncan's multiple range test ($p=0.05$). Bars associated with mean values indicate standard error of mean.

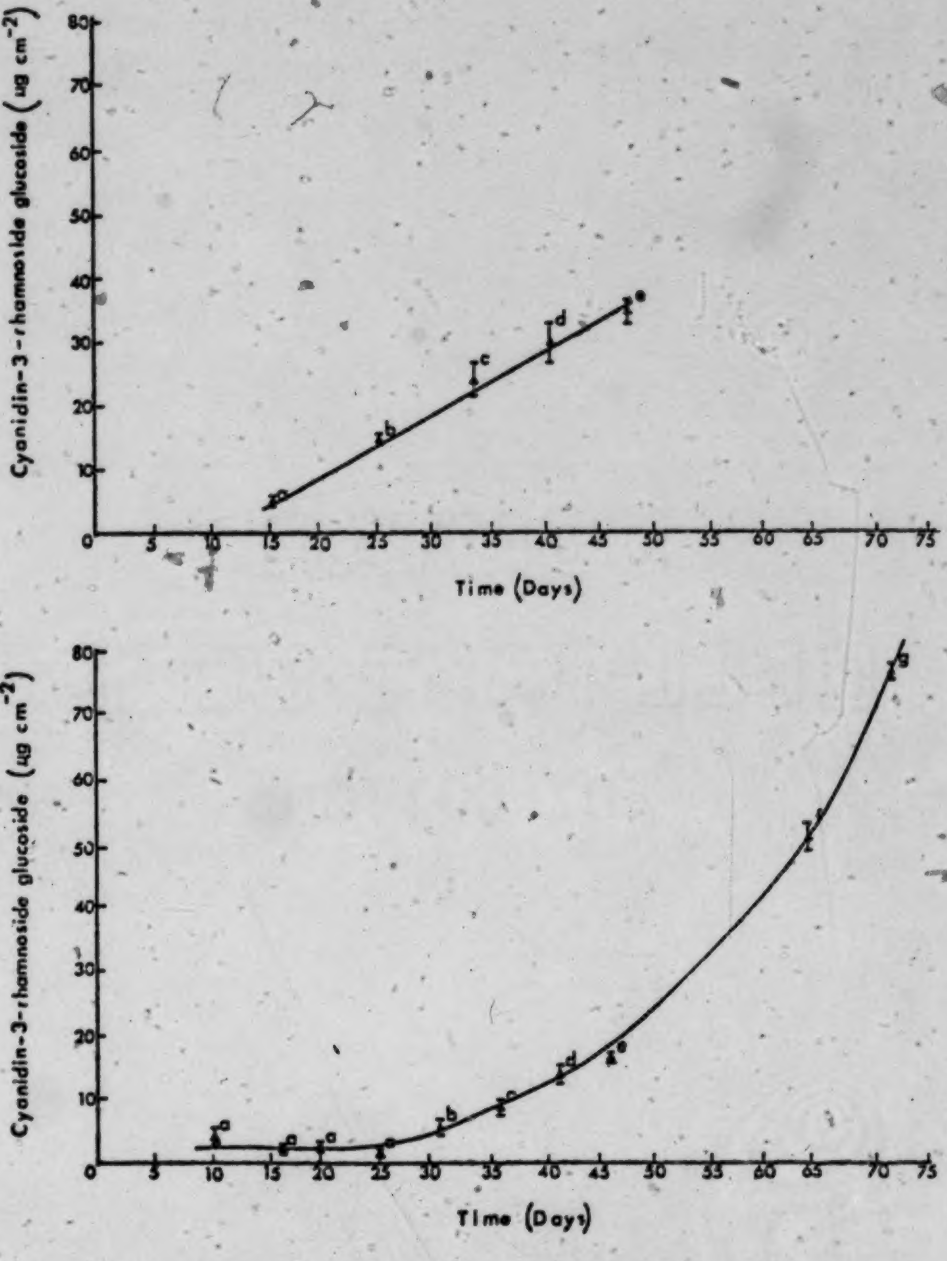


Figure 22. Increase in anthocyanin content[1] in leaves of EG *E. alata* Sieb.'Compacta' exposed to temperatures of 15°C/2°C and a photoperiod of 13 hours (22-1)and 18 hours (22-2).

[1] Mean values used to plot each curve when not followed by a letter in common are significantly different according to Duncan's multiple range test ($p=0.05$). Bars associated with mean values indicate standard error of mean.

hour photoperiod (77.3663 ± 1.2683 µg cy-3-rh glu and 33.126 ± 2.0122 µg cy-3-rh glu cm^{-2} leaf tissue, respectively).

There are several possible reasons for the higher anthocyanin levels reached in plants under the 18 hour photoperiod. Firstly, plants in 18 hour days were exposed to 15°C/2°C for approximately 2 weeks longer before rapid leaf senescence started. Increases in simple sugars and anthocyanin are often correlated with a decrease in starch under cool conditions (Kramer and Kozlowski 1960, Harborne et al 1975). Sugars are known to form the B-ring of the anthocyanin molecule and have been correlated, on numerous occasions, with anthocyanin production when exogenously applied (Creasy 1974, Harborne et al 1975). Therefore, the additional 2 weeks of cool conditions to which plants in the 18 hour photoperiod treatment were exposed could have resulted in conversion of larger quantities of starch to sugars. If higher concentrations of sugars cause higher concentrations of anthocyanin this would have then provided more substrate for anthocyanin synthesis. This difference in anthocyanin levels could also be due to the larger total amount of light received daily by plants in the 18 hour photoperiod treatment, however, no substantial affect is likely from of the 5 hours of light used for photoperiodic extension because light intensity was very low. A third possible reason for increased anthocyanin buildup under long days is that anthocyanin synthesis responds to long photoperiods per se. Schumacher (1966) reports that this is the case in Perilla, Perilla frutescens 'Crispa'.

Since both the 13 and 18 hour photoperiods strongly influenced leaf senescence, it was important to find out how these contributed to the effects of both Eastern and Western conditions on autumn coloration. The Western photoperiod treatment (18 hours for 2 weeks, then 13 hours), when compared to the Eastern photoperiod treatment (13 hours), caused a delay in senescence and abscission of leaves. Changes in chlorophyll and anthocyanin content of senescing leaves from both treatments are shown in Figure 23 and 24 respectively.

Chlorophyll degradation was initiated at approximately the same time in both the Western and Eastern photoperiod treatments. The exact date the increase in anthocyanin was initiated is not known, however, as anthocyanin concentration in both photoperiod treatments had begun to increase by the time analysis for this constituent was started.

Pigment changes in the two photoperiod treatments parallelled one another from the time of their initiation until the time leaf abscission occurred in the Eastern photoperiod treatment. Abscission in the Western photoperiod occurred 26 days later, yet, in spite of this, there was no further accumulation of anthocyanin. During this same period, however, chlorophyll concentration did decrease significantly. There was 22.5% less chlorophyll in leaves of plants in the Western photoperiod treatment at the time of abscission. This difference was statistically significant.

Changes in anthocyanin and chlorophyll content of leaves exposed to simulated conditions indicate, therefore that the additional two weeks of 16-18 hour days typical of the Edmonton environment, should contribute to increased rather than decreased autumn color of _E. alata_ Sieb. 'Compacta'. This effect of the additional two weeks of

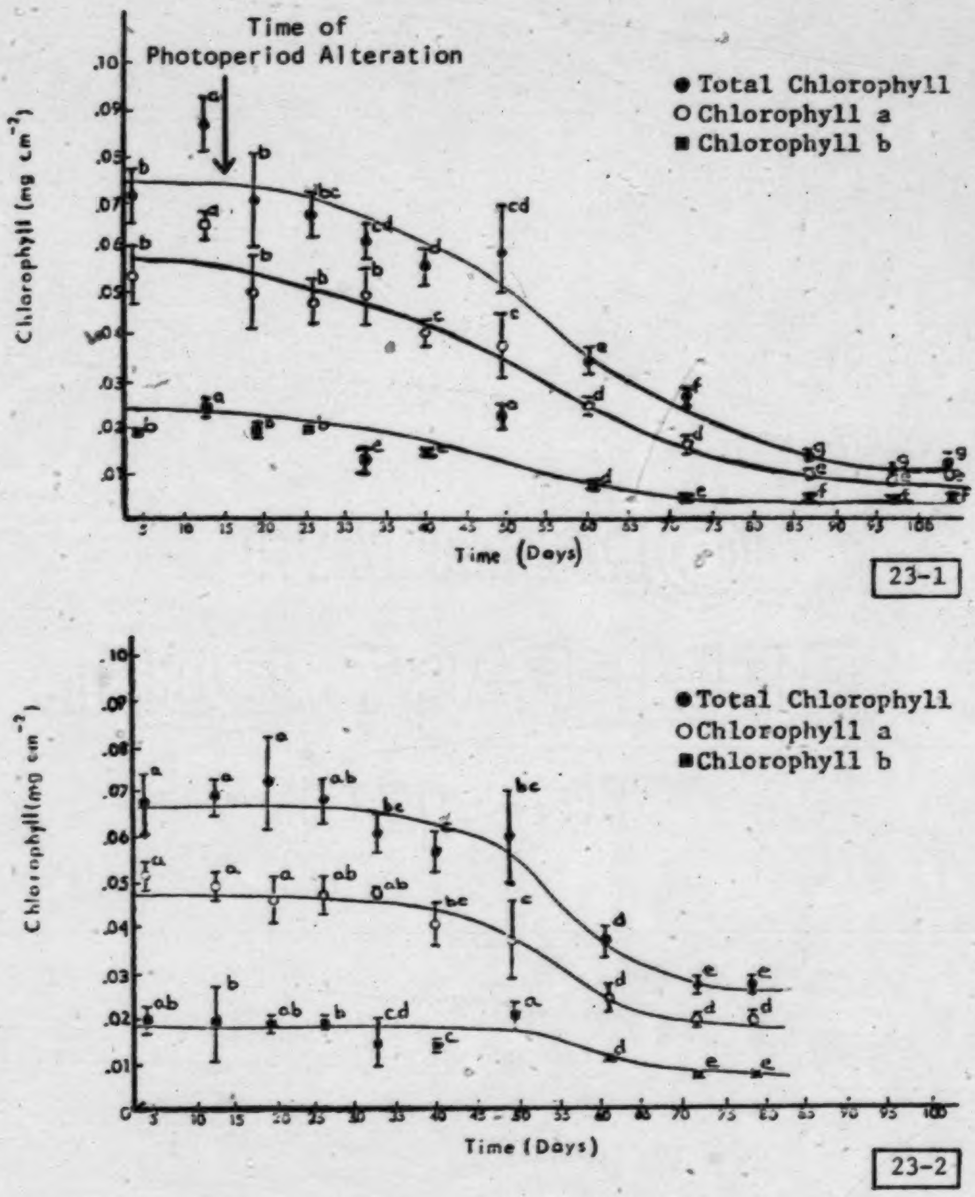


Figure 23. Decline in chlorophyll content[1] in leaves of EG *E. alata* Sieb. 'Compacta' exposed to Western (18 hours for 2 weeks then 13 hours) 23-1 and Eastern (13 hours) photoperiod 23-2. Temperatures held constant at 15°C/2°C.

[1] Mean values used to plot each curve when not followed by a letter in common are significantly different according to Duncan's multiple range test (p=0.05). Bars associated with mean values indicate standard error of mean.

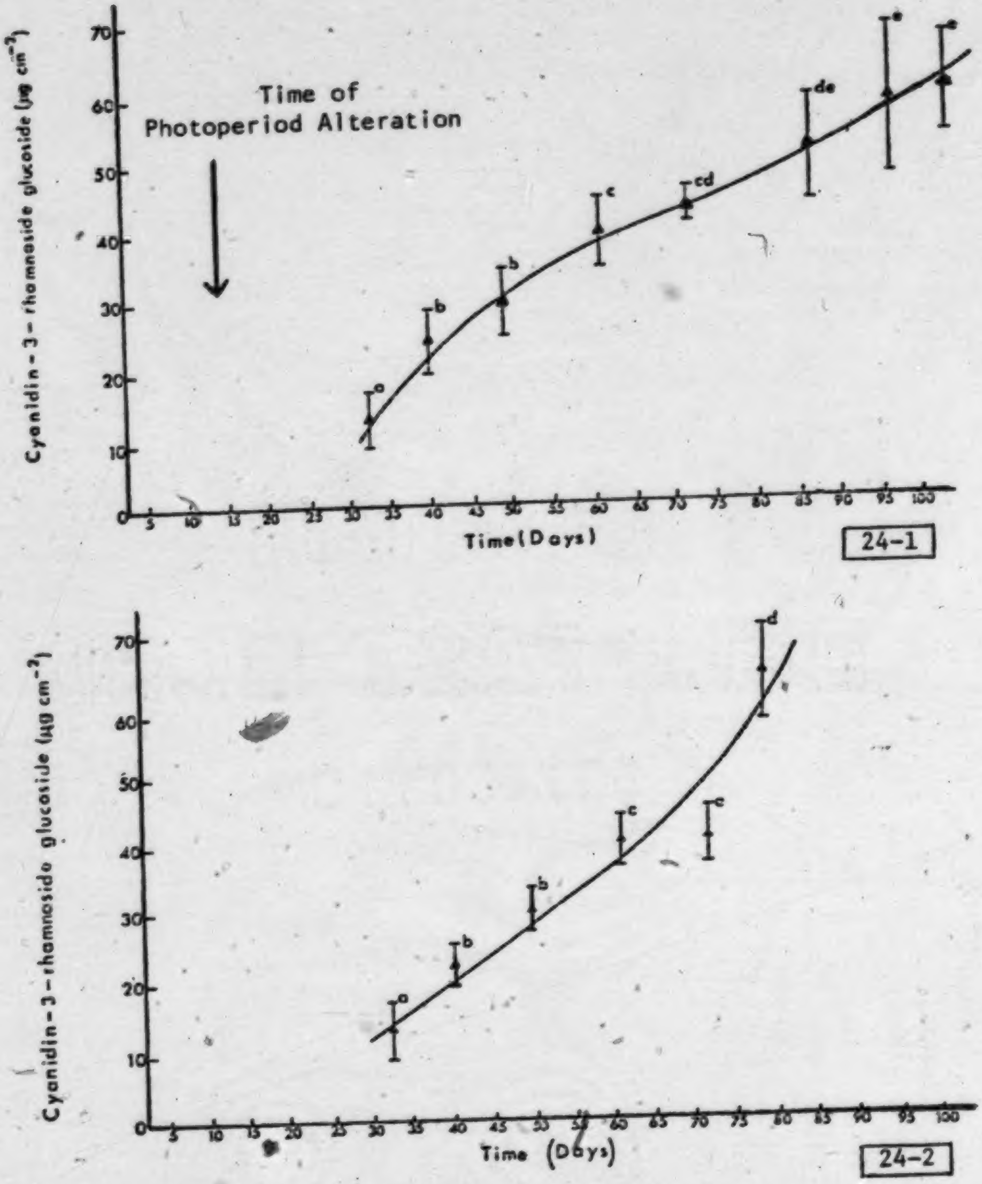


Figure 24. Increase in anthocyanin content[1] in leaves of EG *E. alata* Sieb. 'Compacta' exposed to Western (18 hours for 2 weeks then 13 hours) 24-1 and Eastern (13 hours) photoperiod 24-2. Temperatures held constant at 15°C/2°C.

[1] Mean values used to plot each curve when not followed by a letter in common are significantly different according to Duncan's multiple range test ($p=0.05$). Bars associated with mean values indicate standard error of mean.

16-18 hour days in Edmonton was probably not manifested in the field because temperatures were low enough to prevent extensive degradation of chlorophyll before leaf abscission.

C. Light Quality

All processes of senescence in EG potted plants were influenced by the ratio of far-red:red light during the light period. The effects of a high (1.7) and a low (<0.5) far-red:red light ratio on chlorophyll degradation are shown in Figure 25 and on anthocyanin accumulation in Figure 26.

Initially, chlorophyll content was lower and anthocyanin content was slightly higher in plants exposed to a far-red:red light ratio of 1.7 because the plants used in this treatment were slightly older. These initial differences in pigment content were not felt to detract from the significance of the treatment since the changes in pigment content over time were of primary importance.

The chlorophyll in leaves of plants exposed to a far-red:red light ratio of 1.7 began to decline gradually after approximately 5 to 10 days. The final concentration of chlorophyll just prior to leaf abscission decreased to 0.0086 ± 0.0042 mg cm^{-2} of leaf tissue. Chlorophyll content in leaves of plants exposed to the ratio of less than 0.5, however, did not begin to change until after 22 days of treatment, when the decline was sharp. The final concentration of chlorophyll here was 0.0142 ± 0.0021 mg cm^{-2} leaf tissue, significantly more than in leaves of the other light quality treatment. Leaves of plants exposed to a far-red:red light ratio of 1.7 took 65 days to abscise while those of plants exposed to a ratio less than 0.5 completed abscission in 47 days.

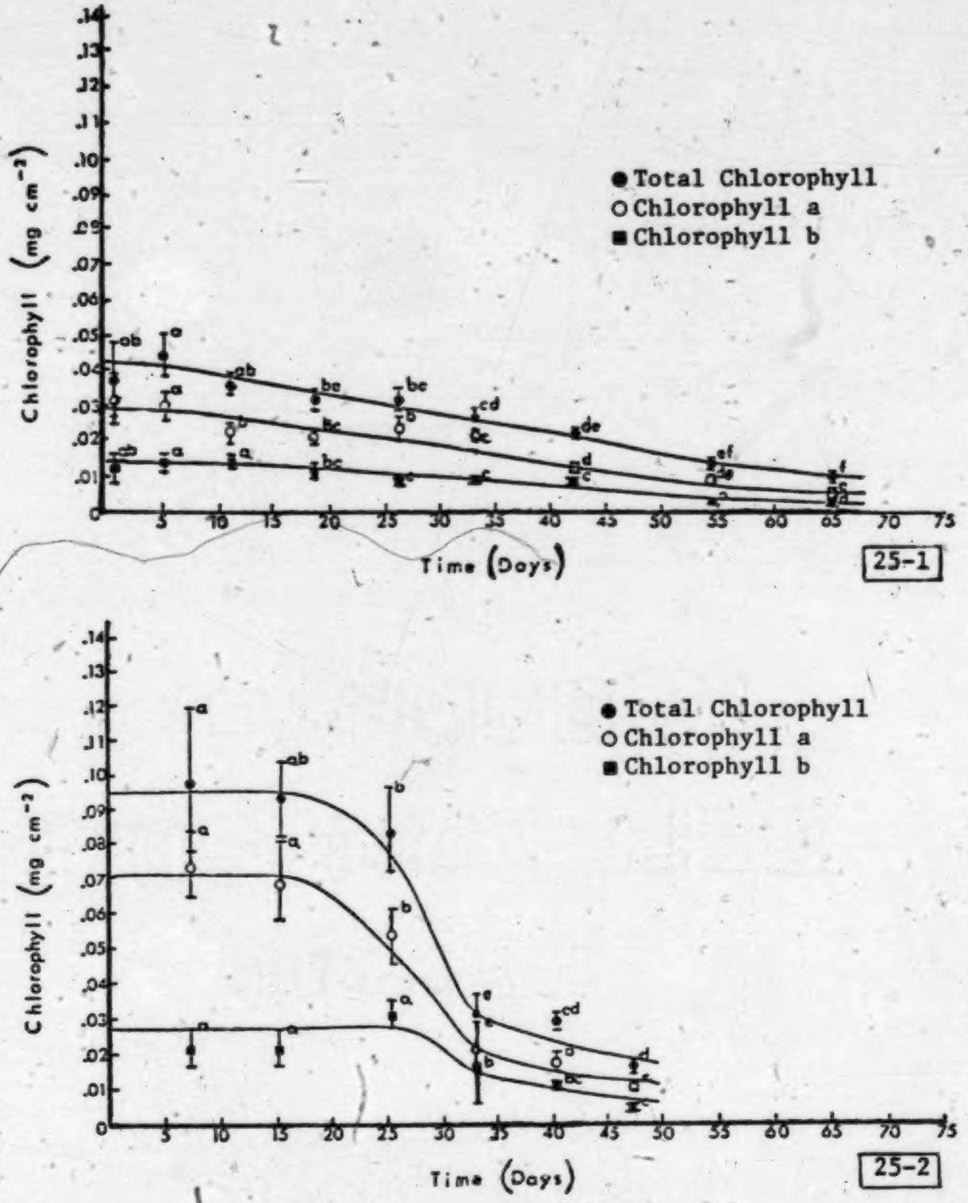


Figure 25. Decline in chlorophyll content[1] in leaves of EG *E. alata* Sieb. 'Compacta' exposed to temperatures of 15°C/2°C, a 13 hour photoperiod and a far-red:red light ratio of 1.7 (25-1) and less than 0.5 (25-2).

[1] Mean values used to plot each curve when not followed by a letter in common are significantly different according to Duncan's multiple range test ($p=0.05$). Bars associated with mean values indicate standard error of mean.

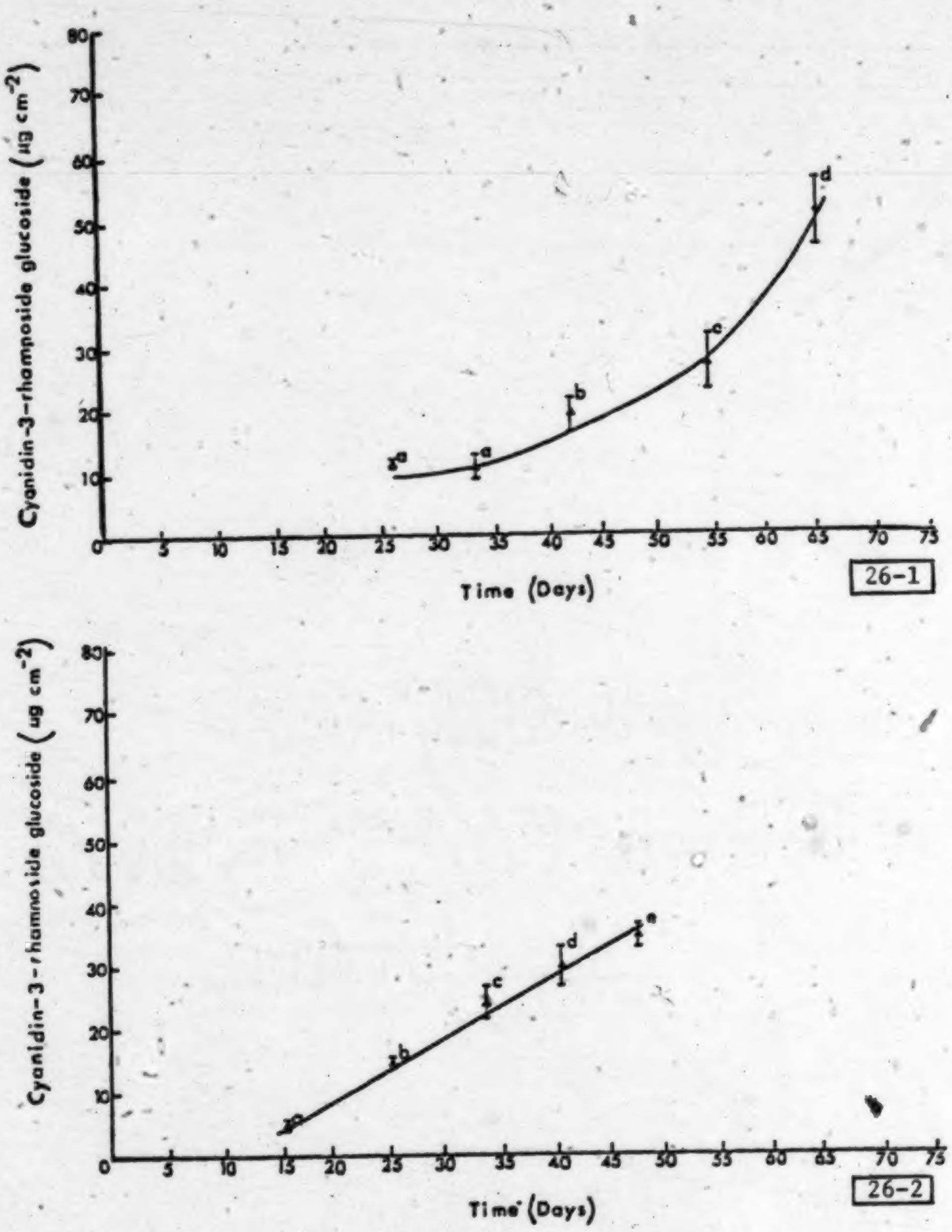


Figure 26. Increase in anthocyanin content[1] in leaves of EG *E. alata* Sieb. 'Compacta' exposed to temperatures of 15°C/2°C and a 13 hour photoperiod. Far-red;red light ratios 1.7 (26-1), less than 0.5 (26-2).

[1] Mean values used to plot each curve when not followed by a letter in common are significantly different according to Duncan's multiple range test ($p=0.05$). Bars associated with mean values indicate standard error of mean.

Anthocyanin accumulation was also initiated at different times in the two light quality treatments. It took more than twice as long (33 days versus 15 days) for anthocyanin accumulation to begin when plants were exposed to the higher far-red:red light light ratio. Furthermore,the final level of anthocyanin reached in the treatment with the higher far-red:red ratio (51.6832 ± 5.0201 μg cy-3-rh glu cm^{-2} leaf tissue) was significantly higher than that reached in the lower (33.1264 ± 2.0122 μg cy-3-rh glu cm^{-2} leaf tissue).

The results of these light quality treatments indicate that the ratio of far-red:red light does influence leaf abscission and pigment change during senescence. The ratio of far-red:red light of 1.7 is very similar to that occurring naturally during autumnal twilight in Edmonton (van Zinderen Bakker 1974). According to Robertson (1966), who states that the ratio of far-red:red light decreases with decreasing latitude, the ratio of far-red:red light occurring in Southern Ontario during autumnal twilight would be less than this. Provided the ratio of far-red:red light affects leaf senescence and abscission in a similar manner when applied only at twilight rather than throughout the light period, then the differences in this environmental parameter must be considered an important contributing factor to the expressed regional differences in autumn coloration. If chlorophyll degradation started earlier in Western Canada, that is, well before the onset of critical low temperatures which were found to halt the process, then Western grown plants might well show better autumn color than their Eastern grown counterparts.

End-of-day light quality has been shown to affect plant growth and metabolism and might be expected to affect leaf senescence. For example, Kasperbauer et al (1970) found that tobacco plants given 5 minutes of far-red light at the end of each day were morphologically distinct from those given 5 minutes of red light at the end of each day. William et al (1972) found that end-of-day treatment of dogwood, Cornus stolonifera with far-red light promoted growth cessation and dormancy.

III. Senescence Response of Leaf Types

A. Field Experiments

EG and WG plants gave quite different senescence responses to Western autumnal conditions in the field. Changes in chlorophyll and anthocyanin content over time are shown in Figures 27 and 28 respectively.

In leaves of WG plants chlorophyll began to decline steadily from approximately October 6, 1976 until leaf abscission 21 days later with final total chlorophyll concentration 34.5% of the initial value.

The process of chlorophyll degradation was more sensitive to change in temperature in leaves of EG plants. Chlorophyll in these plants did not drop steadily but in stages related to changes in temperature. Chlorophyll content just prior to leaf abscission 34 days later was 42.7% of the initial value, significantly higher than that of leaves of WG plants.

A relatively high concentration of chlorophyll in both leaf types was noted at the time of abscission. This is probably an effect of the cold Western autumnal temperatures. Leaves of EG field plants

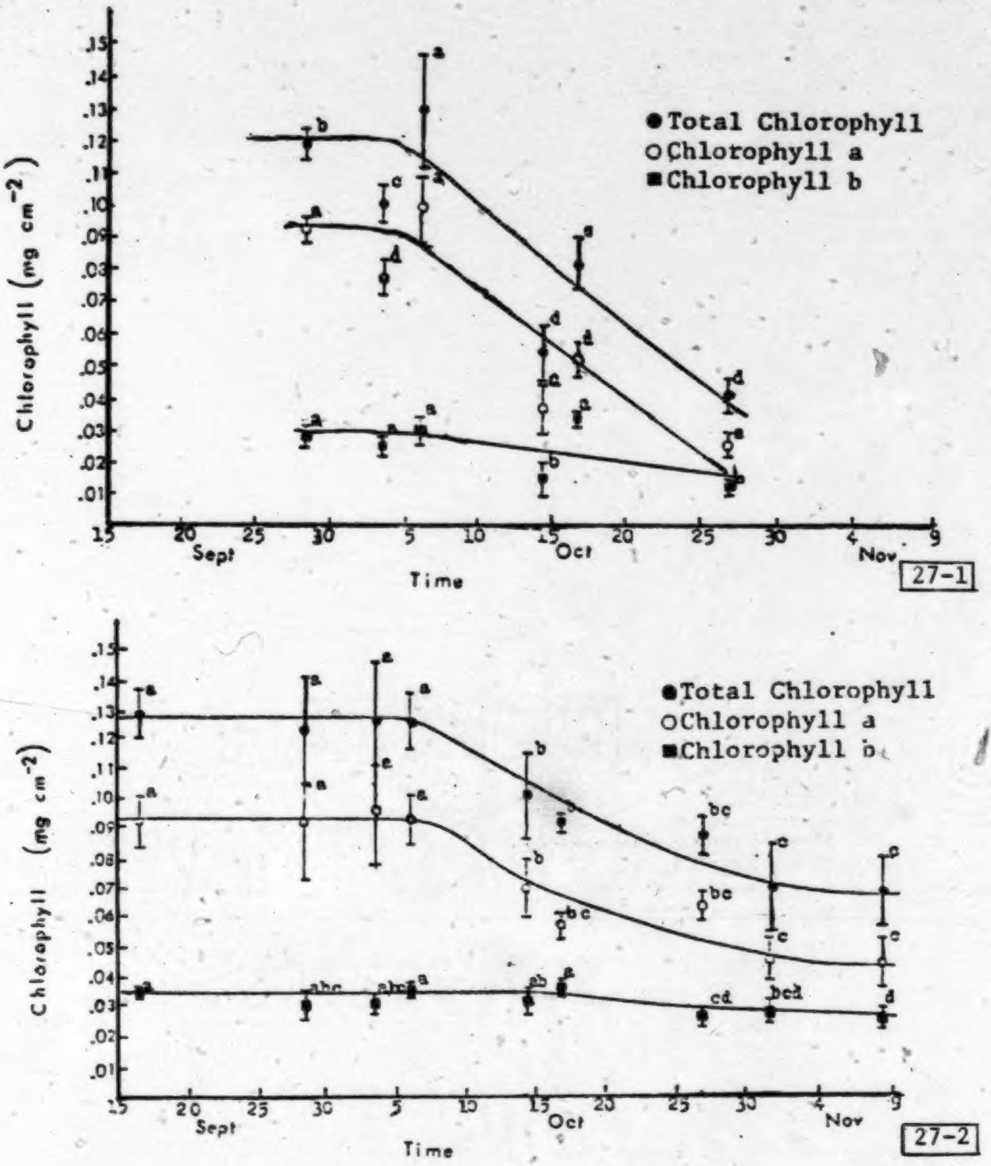
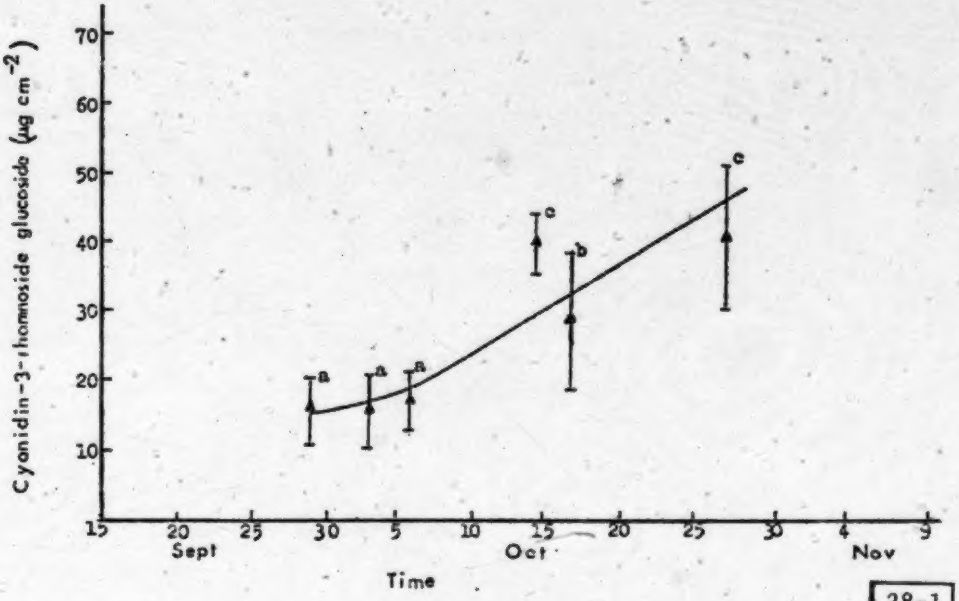
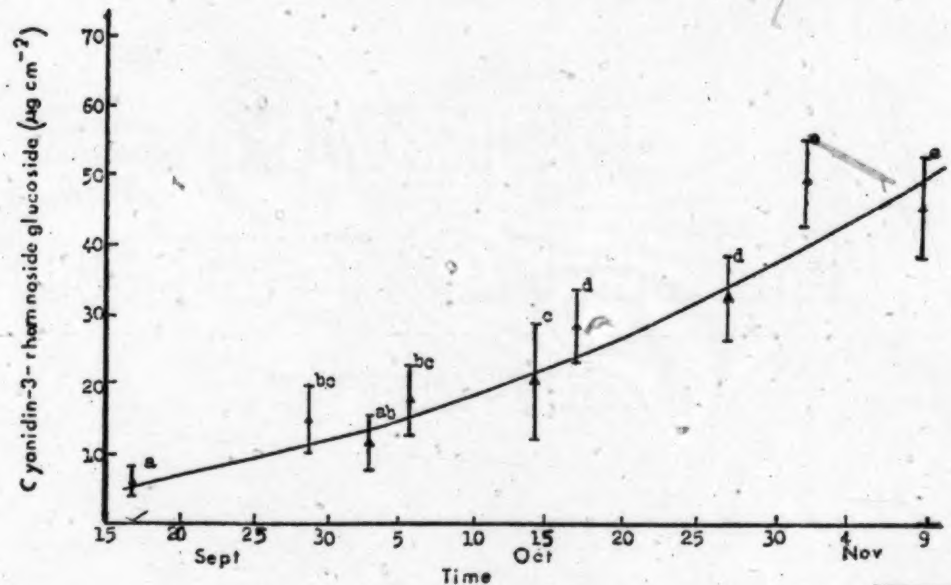


Figure 27. Decline in chlorophyll content[1] in leaves of (27-1) WG and (27-2) EG *E. alata* Sieb. 'Compacta' in the field, September 17 to November 8, 1976.

[1] Mean values used to plot each curve when not followed by a letter in common are significantly different according to Duncan's multiple range test ($p=0.05$). Bars associated with mean values indicate standard error of mean.



28-1



28-2

Figure 28. Increase in anthocyanin content[1] in leaves of (28-1) WG and (28-2) EG E. alata Sieb. 'Compacta' in the field, September 17 to November 8, 1976.

[1] Mean values used to plot each curve when not followed by a letter in common are significantly different according to Duncan's multiple range test ($p=0.05$). Bars associated with mean values indicate standard error of mean.

exposed to modified field temperatures (Figure 10 p.71) contained much less chlorophyll at the time of abscission.

Anthocyanin content in leaves of WG plants began to increase rapidly only after October 5, 1976 to reach a final value of 41.1906 ± 10.1497 μg cy-3-rh glu cm^{-2} leaf tissue. In leaves of EG plants, however, anthocyanin content began to increase steadily right from the beginning of the sampling period, September 17, 1976. The final concentration of anthocyanin reached in these leaves was 46.2501 ± 7.1509 μg cy-3-rh glu cm^{-2} leaf tissue, significantly higher than that found in leaves of WG plants. This higher concentration in leaves of the EG plants must be attributed to leaf type rather than to temperature because in an experiment reported earlier, leaves of EG field plants exposed to modified autumnal field temperatures produced similar amounts of anthocyanin. As a result of this and other experiments it appears that the lack of autumn coloration in leaves of the WG field plants, was due to a higher concentration of residual chlorophyll and a lower concentration of anthocyanin.

Figure 27 and 28 are not to imply that abscission occurred earlier in the WG field plants. Leaves in the sampling area abscised earlier in WG plants but overall leaf abscission was greater in EG plants.

b. Controlled Environment Experiments

The difference in senescence responses of leaves of EG and WG plants was consistent in both controlled environment and field experiments. Preliminary experiments, where EG and WG plants were dug from the field and placed under temperatures of 15°C/2°C and a 10 hour photoperiod, showed that leaves of WG plants took approximately 1 1/2 months longer to abscise, and contained much more chlorophyll at the time of abscission. At the end of this period only about one-third of the leaves of WG plants had abscised, the other two-thirds were wine colored and were confined to the lower branches.

Measurements of chlorophyll in leaves of cuttings taken from both WG and EG plants (see Figure 29) supported these preliminary observations. The interesting thing to note here is the marked difference in response of leaves of the two plant types to factors affecting the degradation of chlorophyll. The immediate, slow, almost steady decline shown by WG plants is in striking contrast to the delayed, abrupt and very rapid decline demonstrated by EG plants. Furthermore, leaves of WG plants contained significantly more chlorophyll just prior to abscission than those of EG plants (0.1267 ± 0.0133 mg cm^{-2} leaf tissue versus 0.0526 ± 0.0058 mg cm^{-2} leaf tissue).

In the field, the converse was true in that chlorophyll content in leaves of EG plants was higher prior to abscission than in leaves of WG plants. This result, however, is not felt to be as demonstrative of the senescent response of leaf types as the results of the controlled environment experiments. This is because field temperatures were too low to allow completion of the senescence process.

The distinctly different senescence responses of leaves WG and EG plant types must have been due to the effect of environmental conditions existing during bud initiation. The observed responses could have been due to biochemical and/or previously described morphological differences in leaves of the two plant types.

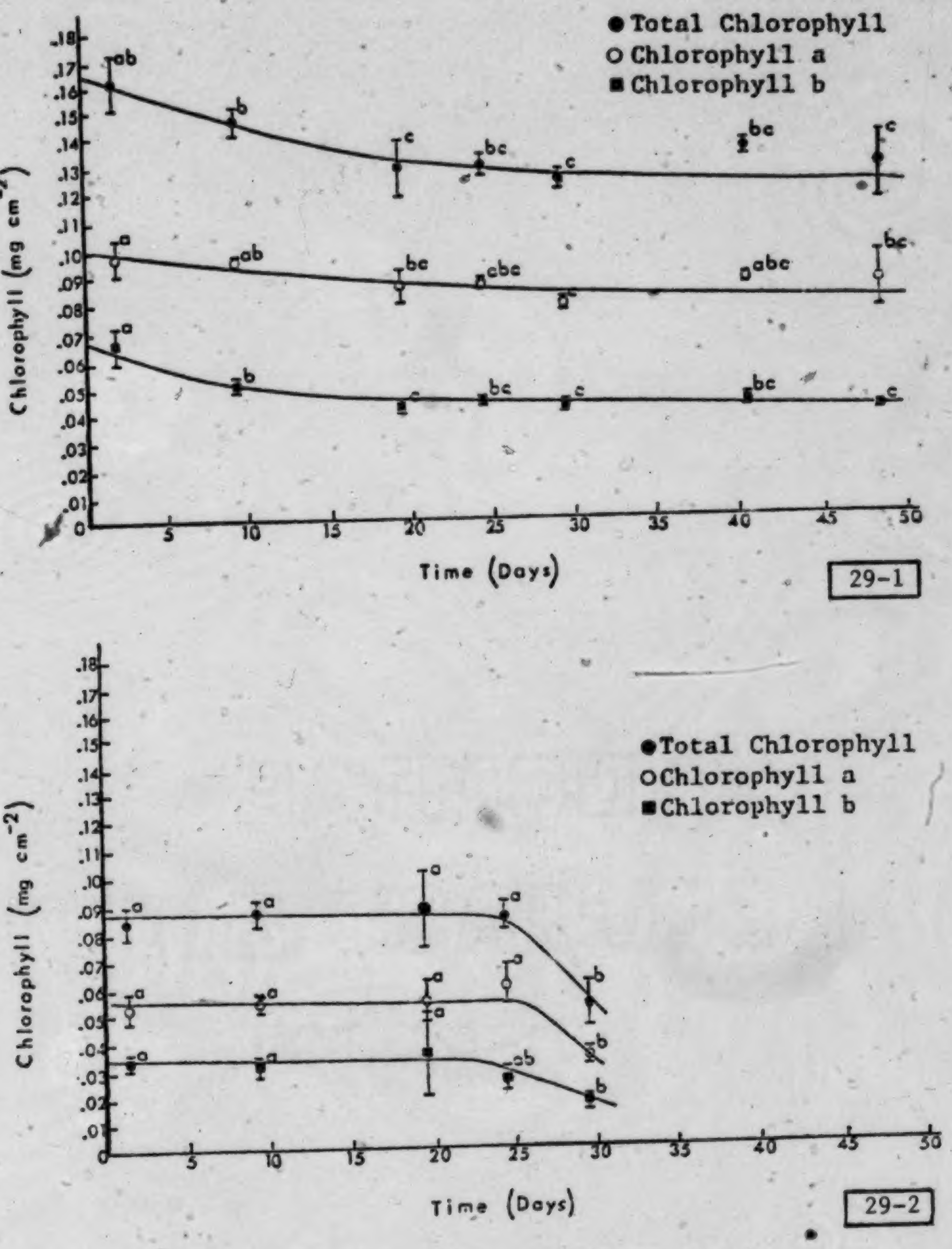


Figure 29. Decline in chlorophyll content[1] in leaves of cuttings taken from (29-2) WG and (29-2) EG *E. alata* Sieb.'Compacta' plants exposed to temperatures of 15 C/2 C and a 13 hour photoperiod.

[1] Mean values used to plot each curve when not followed by a letter in common are significantly different according to Duncan's multiple range test ($p=0.05$). Bars associated with mean values indicate standard error of mean.

In this study, the senescence response of leaves formed under simulated Eastern and Western photoperiods and temperatures were examined. Changes in chlorophyll content were measured in leaves formed in 16 hour days (Eastern photoperiod) at temperatures of 20°C/7°C and 23°C/13°C (Western and Eastern temperatures, respectively) and in 18 hour days (Western photoperiod) at 20°C/7°C (see Figure 30).

The trend in chlorophyll degradation when chlorophyll content was expressed as mg g^{-1} leaf tissue was similar to that when chlorophyll content was expressed as mg cm^{-2} leaf tissue in all treatments (see Appendix 7). Tissues formed under different environmental conditions therefore did not differ in loss of dry weight concomitant with senescence, per unit loss of chlorophyll.

For some unknown reason, chlorophyll concentration in leaves formed in 16 hour days at temperatures of 20°C/7°C and 23°C/13°C rose initially when they were moved to the environmental conditions used to induce senescence (15°C/2°C, 13 hour photoperiod). Following this, the chlorophyll content remained stable until rapid breakdown took place approximately 49 days later. The plants which had formed leaves at 20°C/7°C in 18 hour photoperiods showed no such initial rise in chlorophyll content when moved to the new environment but they did respond in a similar way in that chlorophyll degradation was initiated at approximately the same time.

In these three treatments the number of days to leaf abscission, varied somewhat (Figure 30). Leaves formed under a 16 hour day and temperatures of 23°C/13° took 9 days longer to abscise than those formed under the other treatments. This result does not explain why the leaves of WG plants and cuttings took longer to abscise under

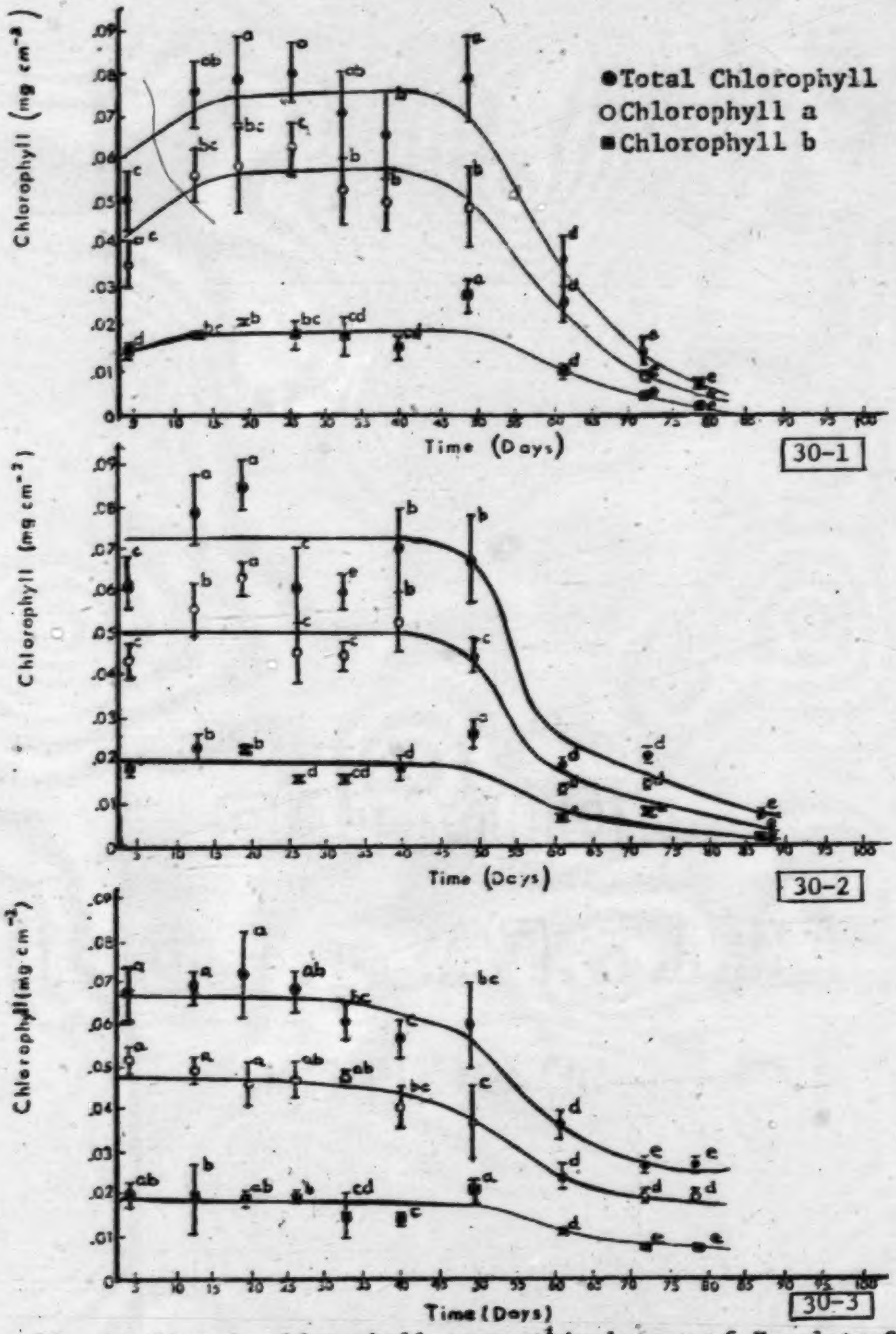


Figure 30. Decline in chlorophyll content[1] in leaves of E. alata Sieb. 'Compacta' formed under (30-1) 20°C/7°C, 16 hour photoperiod, (30-2) 23°C/13°C, 16 hour photoperiod, and (30-3) 20°C/7°C, 18 hour photoperiod.

[1] Mean values used to plot each curve when not followed by a letter in common are significantly different according to Duncan's multiple range test ($p=0.05$). Bars associated with mean values indicate standard error of mean.

under controlled environment conditions. However, the results do offer an explanation for the higher concentration of chlorophyll noted in leaves of WG plants at the time of abscission. Leaves formed under conditions simulating those of Western Canada (20°C/7°C, 18 hour photoperiod) contained significantly more chlorophyll at the time of abscission than leaves formed under any other set of conditions (see Tables 11 and 12). It was the effect of the 18 hour photoperiod that produced this result. This is obvious by comparing Treatments 1 and 2 and Treatments 1 and 3 listed in Tables 11 and 12. Chlorophyll content just prior to abscission was not significantly different in leaves formed under a 16 hour photoperiod and temperatures of either 20°C/7°C or 23°C/13°C whereas this was not the case when temperature was held at 20°C/7°C and photoperiod was either 13 or 18 hours.

The percentage drop in chlorophyll was less when expressed as mg g^{-1} leaf tissue than as mg cm^{-2} leaf tissue. This is obviously due to decline of both tissue weight and pigment concentration, during leaf senescence.

A comparison of Treatments 1 and 4 (Tables 11 and 12), indicate that the reduced light intensity (380 $\mu E\ m^{-2}s^{-1}$) during leaf development of plants in the 20°C/7°C, 18 hour photoperiod did not affect chlorophyll degradation.

Anthocyanin accumulation also differed in leaves of plants formed under the various environmental conditions (Figures 31). In all cases, however, the maximum rate of accumulation occurred when the rate of chlorophyll degradation was proceeding most rapidly.

Table 11. Chlorophyll content (just prior to abscission) expressed as mg cm^{-2} leaf tissue. Photoperiod and temperature treatments used to simulate growing conditions in Eastern and Western Canada.

Treatment No.	Conditions simulated during leaf growth	Chlorophyll Content[+]					
		Chlorophyll a		Chlorophyll b		Total Chlorophyll	
		mg cm^{-2}	% of initial content[++]	mg cm^{-2}	% of initial content[++]	mg cm^{-2}	% of initial content[++]
1	Western temperatures (20°C/ 7°C); Eastern photoperiod (16 hours), (PAR-420 µE m^{-2} s^{-1})	0.005 a	8.8	0.002 a	11.8	0.007 a	9.3
2	Eastern temperatures (23°C/ 13°C); Eastern photoperiod (16 hours), (PAR-420 µE m^{-2} s^{-1})	0.005 a	10.0	0.002 a	10.0	0.007 a	9.7
3	Western temperaures (20°C/ 7°C); Western photoperiod (18 hours), (PAR-380 µE m^{-2} s^{-1})	0.019 b	39.6	0.007 b	38.9	0.026 b	38.8
4	Western temperatures (20°C/ 7°C); Eastern photoperiod (16 hours), (PAR-380 uE m^{-2} s^{-1})	0.006 a	10.9	0.002 a	10.0	0.008 a	10.8

[+] Mean values within each column when not followed by a letter in common, are significantly different according to Duncan's multiple range test ($p=0.05$).

[++] The stable period of chlorophyll content before breakdown in all treatments was used to approximate initial chlorophyll concentrations.

Table 12. Chlorophyll content (just prior to abscission) expressed as mg g^{-1} leaf tissue. Photoperiod and temperature treatments used to simulate growing conditions in Eastern and Western Canada.

Treatment No.	Conditions simulated during leaf growth	Chlorophyll Content[+]					
		Chlorophyll a		Chlorophyll b		Total Chlorophyll	
		mg g^{-1}	% of initial content[++]	mg g^{-1}	% of initial content[++]	mg g^{-1}	% of initial content[++]
1	Western temperatures (20°C/ 7°C); Eastern photoperiod (16 hours) (PAR-420 $\mu E\ m^{-2}\ s^{-1}$)	0.47 a	12.7	0.21 a	15.4	0.69 a	14.1
2	Eastern temperatures (23°C/ 13°C); Eastern photoperiod (16 hours) (PAR-420 $\mu E\ m^{-2}\ s^{-1}$)	0.60 a	13.0	0.27 b	13.5	0.85 a	13.9
3	Western temperaures (20°C/ 7°C); Western photoperiod (18 hours) (PAR-380 $\mu E\ m^{-2}\ s^{-1}$)	1.40 b	53.8	0.55 c	50.0	1.96 c	56.0
4	Western temperatures (20°C/ 7°C); Eastern photoperiod (16 hours) (PAR-380 $\mu E\ m^{-2}\ s^{-1}$)	0.51 a	14.6	0.21 a	17.5	0.72 a	15.0

[+] Mean values within each column when not followed by a letter in common, are significantly different according to Duncan's multiple range test ($p=0.05$).

[++] The stable period of chlorophyll content before breakdown in all treatments was used to approximate initial chlorophyll concentrations.

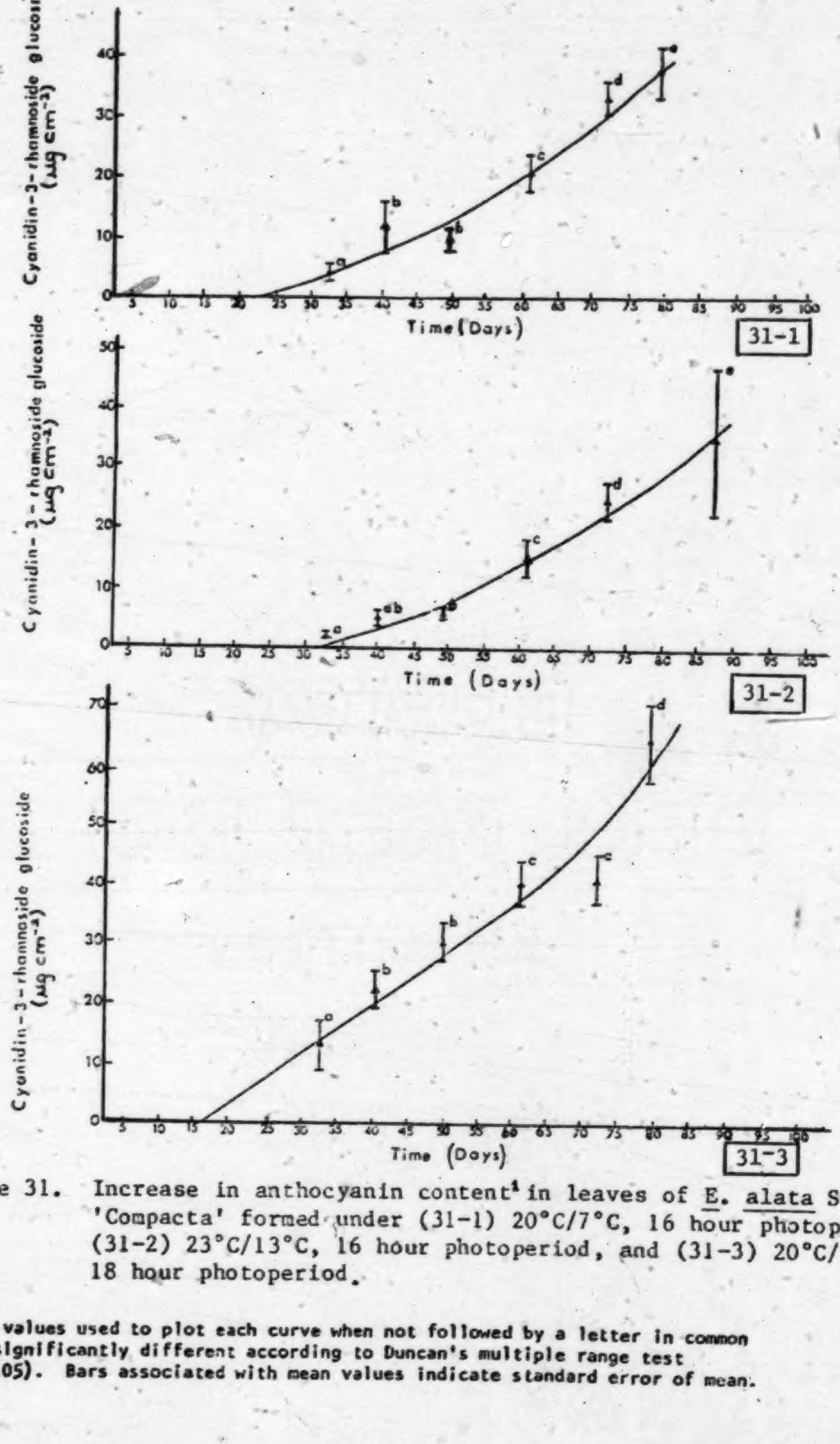


Figure 31. Increase in anthocyanin content[1] in leaves of E. alata Sieb. 'Compacta' formed under (31-1) 20°C/7°C, 16 hour photoperiod, (31-2) 23°C/13°C, 16 hour photoperiod, and (31-3) 20°C/7°C, 18 hour photoperiod.

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[1] Mean values used to plot each curve when not followed by a letter in common are significantly different according to Duncan's multiple range test ($p = 0.05$). Bars associated with mean values indicate standard error of mean.

Anthocyanin content at the time of leaf abscission was highest in leaves formed under 20°C/7°C and an 18 hour photoperiod (see Table 13). This effect was obviously due to the influence of the longer day rather than the cooler temperatures on leaf formation. Anthocyanin content just prior to leaf abscission was not significantly different in leaves formed in 16 hour days at either temperature. However, when temperatures were held at 20°C/7°C, the anthocyanin content was significantly greater in leaves formed under the longer photoperiod. The 18 hour day may therefore have allowed a greater buildup of anthocyanin substrate than the 16 hour day. In extrapolating these results to what occurred in the field, this higher concentration of anthocyanin at the time of abscission would certainly not be a factor contributing to reduced autumn coloration in Edmonton.

Table 13. Anthocyanin content just prior to abscission of leaves formed under combined photoperiod and temperature treatments used to simulate growing conditions in Eastern and Western Canada.

Treatment No.	Conditions simulated during leaf growth	Anthocyanin Content+	
		ug cy-3-rh glu cm^{-2}	mg cy-3-rh glu g^{-1}
1	Western temperatures (20°C/7°C) Eastern photoperiod (16 hours) (PAR-420 $\mu E\ m^{-2}\ s^{-1}$)	37.0694 ± 4.5969 a	3.5779 ± 0.2525 a
2	Eastern temperatures (23°C/13°C) Eastern photoperiod (16 hours) (PAR-420 $\mu E\ m^{-2}\ s^{-1}$)	35.3993 ± 2.2115 a	3.5714 ± 0.1418 a
3	Western temperatures (20°C/7°C) Western photoperiod (18 hours) (PAR-380 $\mu E\ m^{-2}\ s^{-1}$)	64.6408 ± 7.8408 b	4.9823 ± 0.5446 a
4	Western temperatures (20°C/7°C) Eastern photoperiod (16 hours) (PAR-380 $\mu E\ m^{-2}\ s^{-1}$)	38.1077 ± 6.1422 a	3.4773 ± 0.4129 a

+ Mean values within each column when not followed by a letter in common are significantly different according to Duncan's multiple range test ($p=0.05$).

CONCLUSIONS AND SUMMARY

This study isolated several factors contributing to the difference in autumn coloration of E. alata Sieb. 'Compacta' growing in Edmonton (Western Canada) and in Southern Ontario (Eastern Canada).

Firstly, leaves that had been initiated under environmental conditions specific to each region differed morphologically anatomically, and in their senescence response. Leaves of field plants which were initiated and expanded under Western conditions were thicker and had a greater development of palisade parenchymatous tissue than leaves initiated in Eastern, but expanded under Western, conditions. Knowles (personal communication) had also observed similar leaf types on plants growing in Eastern and Western Canada.

Controlled environment experiments indicated that regional differences in temperature and photoperiod contribute to the observed difference in leaf anatomy. Leaves of EG plants that had expanded and matured under simulated Western conditions (20°C/7°C, 18 hour photoperiod) had a greater amount of palisade parenchymatous tissue than leaves expanded and matured under simulated Eastern conditions (29°C/13°C, 16 hour photoperiod). The longer day of the simulated Western environment was more important in this respect than was temperature.

The senescence response of leaf types also differed. In most cases, leaves formed under Western conditions contained more chlorophyll just prior to abscission and thus displayed less brilliant autumn color than leaves formed under Eastern conditions. For example, in controlled experiments when temperatures were favorable for development of autumn coloration (15°C/2°C), leaves of WG plants had a higher concentration of chlorophyll just prior to abscission than leaves of EG plants. Leaves of EG plants formed under simulated Western conditions (20°C/7°C, 18 hour photoperiod) not only contained more chlorophyll prior to abscission but also more anthocyanin than leaves formed under simulated Eastern conditions (23°C/13°C, 16 hour photoperiod). Again, this difference was due to the longer days of the Western treatment rather than to cooler temperatures.

The number of days until completion of leaf abscission under conditions favorable to senescence (15°C/2°C, 13 hour photoperiod), also varied with leaf type. Leaves of WG plants dug from the field generally took longer to abscise. However, when leaves of EG plants, formed under simulated Eastern conditions (23°C/13°C, 16 hour photoperiod) were moved to conditions favorable for senescence they took 9 days longer to abscise than those formed under simulated Western conditions (20°C/7°C, 18 hour photoperiod). Further experimentation is necessary to draw definite conclusions on the effect of Eastern and Western environments on leaf abscission in E. alata Sieb. 'Compacta'.

Environmental conditions during leaf senescence as well as during leaf development were found to influence the development of autumn color. Both field and controlled environment studies indicated that the minimum temperature to which plants growing in Edmonton were exposed, adversely affected coloration. This was largely due to the effect on chlorophyll degradation. Chlorophyll degradation in field plants was increased by preventing autumnal minimum temperatures from dropping to their normal levels. Under controlled environment conditions, plants exposed to temperatures simulating the autumn temperatures of Eastern Canada (15°C/5°C) colored up well while those exposed to simulated Western autumnal temperatures (15°C/0°C/-5°C) did not. Anthocyanin synthesis as well as chlorophyll degradation was increased in plants exposed to temperatures simulating Eastern conditions. Temperatures midway between those of simulated Eastern and Western conditions, viz 15°C/2°C, produced autumn color intermediate to that observed in each temperature treatment.

Autumnal temperatures were also found to influence leaf abscission. Under controlled environment conditions leaf abscission was completed in 44 days in the Eastern temperature treatment (15°C/5°C), in 47 days in the 15°C/2°C temperature treatment and in 50 days in the Western temperature treatment (15°C/0°C/-5°C). In the field, leaf abscission occurred more readily on plants exposed to minimum temperatures that had been raised a few degrees above those occurring normally. Anatomical investigation, however, could not discern observable differences in development of the abscission layer in plants exposed to either of the field temperature treatments.

Modified and noncontrolled field temperatures did not differentially influence the only other senescence phenomenon studied, that of increasing α-amino nitrogen content.

Senescence responses of E. alata Sieb. 'Compacta' were also found to be photoperiod sensitive. When temperatures were conducive to promoting senescence (15°C/2°C), an 18 hour day delayed both leaf senescence and abscission over that noted in a 13 hour day. There was little or no chlorophyll degradation in an 18 hour day, however, a greater amount of anthocyanin acumulated. The photoperiod treatment used to simulate Western conditions (18 hours for 2 weeks, then 13 hours) also delayed leaf abscission over that used to simulate Eastern conditions (13 hours). These differences produced by autumnal photoperiods in the two regions are not believed to contribute to variation in autumn coloration. Anthocyanin concentration just prior to leaf abscission was not significantly different in the two treatments but there was significantly less chlorophyll in leaves of plants in the Western photoperiod treatment just prior to abscission.

Changes in chlorophyll and anthocyanin content over time, as well as their levels just prior to leaf abscission, are important in considering the reasons why the Western photoperiod was not an important contributor to autumn coloration. Changes in concentration of the two pigments in the two photoperiod treatments paralleled one another from the time of their initiation until leaf abscission occurred in the Eastern photoperiod treatment. Even though leaf abscission occurred much later in the Western photoperiod treatment, little further chlorophyll degradation and no further anthocyanin accumulation occurred in these plants before leaf abscission. As a result of this, the chlorophyll content in plants of both treatments was the same at the time the leaves of plants in the Eastern treatment abscised. Since low temperatures would halt further degradation of chlorophyll in plants in the field under Western conditions, then the Western photoperiod treatment can be considered as having no value in promoting further autumn coloration.

The ratio of far-red:red light during the day influenced chlorophyll degradation, anthocyanin accumulation, and abscission of leaves under controlled environment conditions. Plants exposed to a far-red:red light ratio of 1.7 during the light period, when temperatures were held at 15°C/2°C and photoperiod was 13 hours, took longer to abscise than those exposed to a ratio less than 0.5. Leaves from the former treatment also contained significantly more anthocyanin and significantly less chlorophyll just prior to abscission than those from the latter.

If ratios of far-red:red light similar to these, delayed leaf senescence and abscission when applied only at day-end, then light quality may contribute to the difference in autumn coloration of this plant in Edmonton and Southern Ontario. A ratio of far-red:red light similar to 1.7 occurs during periods of autumnal twilight in Edmonton. The ratio during periods of autumnal twilight in Southern Ontario is somewhat lower than this. In this experiment, changes in chlorophyll content in the two treatments did not parallel one another closely. In the treatment with the higher far-red:red light ratio, chlorophyll was degraded slowly and continuously until the time of leaf abscission. This is in contrast with the abrupt and rapid decrease in chlorophyll content in leaves of plant exposed to the lower ratio of far-red:red light. In the case of leaves exposed to a far-red:red light ratio of 1.7, a reduction or outright cessation of chlorophyll degradation by exposure to lower Western autumnal temperatures would occur in leaf tissue with a higher concentration of chlorophyll (and thus less autumn color) than in similar tissue from plants growing in Eastern Canada.

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APPENDIX 1. Average monthly total and net solar radiation from March to November for Edmonton, Ottawa, and Toronto

Average monthly total solar radiation[1] (Environment Canada 1965 - 1974) from March to November for Edmonton, Ottawa and Toronto.

	TOTAL SOLAR RADIATION[2] (LANGLEYS)					
	EDMONTON		OTTAWA		TORONTO	
MONTH	AVE	STND. DEV.	AVE	STND. DEV.	AVE	STND. DEV.
Mar	307.90	± 33.42 cde	313.10	± 38.51 cde	307.50	± 34.15 cde
Apr	420.10	± 26.21 fg	397.10	± 19.92 ghi	403.10	± 27.66 fg
May	502.70	± 37.94 jkl	456.30	± 54.41 lmn	474.60	± 51.52 jk
June	518.50	± 52.75 n	489.00	± 58.57 mn	577.00	± 57.36 km
July	530.80	± 35.66 mn	502.20	± 44.73 n	526.50	± 39.40 lmn
Aug	442.40	± 26.00 ijk	411.70	± 24.18 hij	454.70	± 22.24 fgh
Sept	290.80	± 31.29 cde	308.90	± 25.83 c	319.80	± 67.99 cde
Oct	185.30	± 21.85 b	195.80	± 19.77 b	218.70	± 30.34 b
Nov	90.90	± 11.87 a	102.80	± 10.59 a	108.30	± 13.89 a

1. Letters indicate results of a Duncan's multiple range test at the 5% level of significance on averages for all months for all cities.
2. Edmonton-measured with a KIPP CM6 pyranometer, Toronto and Ottawa-measured with an Eppley 180 pyranometer.

Average monthly net solar radiation[1] (Environment Canada 1965 - 1974) from March to October for Edmonton, Ottawa and Toronto.

	NET SOLAR RADIATION[2] (LANGLEYS)					
	EDMONTON		OTTAWA		TORONTO	
MONTH	AVE	STND. DEV.	AVE	STND. DEV.	AVE	STND. DEV.
Mar	21.67	± 61.65 a	19.00	± 30.65 a	121.88	± 67.11 de
Apr	156.43	± 32.11 ef	154.00	± 16.32 ef	207.13	± 20.99 gh
May	235.88	± 44.45 ch	203.88	± 21.53 ghi	225.63	± 28.15 hij
June	244.75	± 17.79 jk	225.50	± 29.76 hij	271.25	± 32.08 k
July	246.50	± 7.54 jk	223.25	± 41.51 hij	276.88	± 13.78 k
Aug	198.38	± 18.29 ghj	208.50	± 27.68 hi	232.13	± 25.01 hij
Sept	99.00	± 7.84 cd	129.50	± 15.87 de	172.38	± 63.63 fg
Oct	17.88	± 7.68 a	63.38	± 9.38 b	83.75	± 17.32 bc

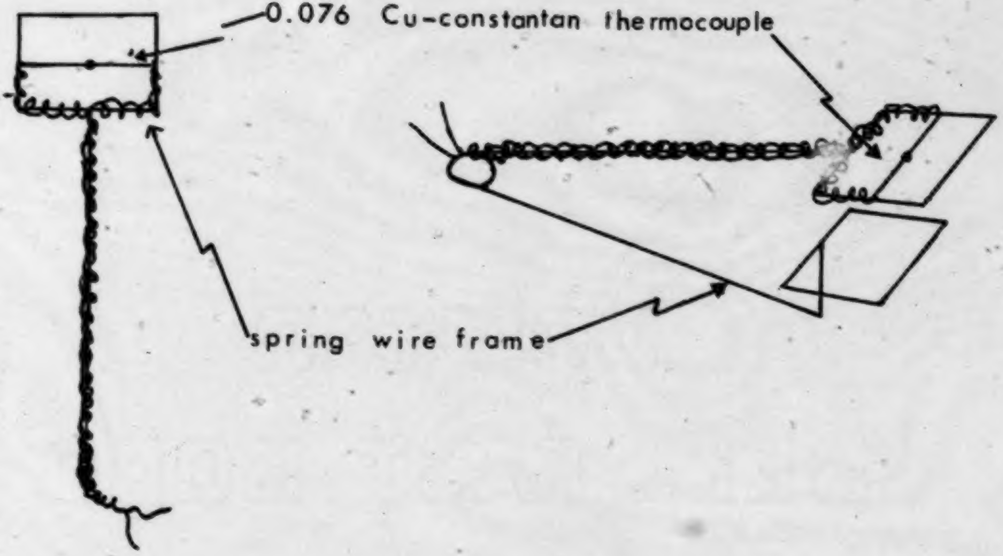
1. Letters indicate results of a Duncan's multiple range test at the 5% level of significance on averages for all months for all cities.
2. Measured with a CSIRO pyrradiometer.

APPENDIX 2. University of California Soil Mix (Baker 1957).

To obtain 1 cubic yard of mix:

1/2 cu. yd. peat
1/2 cu. yd. sand
20 g potassium nitrate
20 g potassium sulphate
25 g superphosphate
800 g calcium-carbonate
600 g magnesium carbonate
714 g Hoof and Horn

APPENDIX 3. Thermocouple used in temperature measurement


0.076 Cu-constantan thermocouple
spring wire frame

APPENDIX 4. Tissue preparation methods used in anatomical investigations of *E. alata* Sieb. 'Compacta'.

A. Tertiary butyl alcohol solutions used in tissue dehydration.

	Solution				
	I	II	III	IV	V
Total percentage of alcohol	50	70	85	95	100
Distilled water (ml)	50	30	15	--	---
95% ethyl alcohol (ml)	40	50	50	45	---
Tertiary butyl alcohol (ml)	10	20	35	55	75
100% ethyl alcohol (ml)	--	--	--	--	25

B. Staining procedure used in anatomical investigation of abscission zone (Esau 1947);

1. Deparaffinized slides were taken from distilled water and soaked for ten minutes in a 4% aqueous ferric ammonium sulphate solution.

2. Slides were washed in distilled water (changed four times in ten minutes).

3. Transferred slides to a weak solution of haematoxylin prepared by putting ten drops of a stock solution (2.5 g haematoxylin in 100 ml of 95% ethanol) into 300 ml distilled water. The mixture was then made slightly alkaline with sodium bicarbonate. Slides were stained for 30 minutes until the cells walls had turned slightly bluish.

4. Slides were then transferred to and stained for twenty hours in a dilute safranin-O solution prepared by adding five drops of a stock solution (1 g safranin-O in 100 ml 50% ethanol) to 300 ml distilled water.

5. Slides were destained in 50% ethanol and dehydrated by transferring to each of the following alcohol solutions, in order, leaving the slides five minutes in each solution: 70% ethanol, 80% ethanol, 100% ethanol, and xylene.

C. Staining procedure used in anatomical investigation of leaf tissue (Johansen 1940).

1. Deparaffinized slides were transferred from 50% alcohol to safranin stain solution for eighteen hours. Safranin solution made as follows: 4 g safranin-O dissolved in 200 ml methyl cellusolve (ethylene glycol monomethyl ether) added to 100 ml 95% ethanol, 100 ml distilled water, 4 g sodium acetate, and 8 ml formalin.

2. Slides were then rinsed in cold water and placed in 95% ethanol containing 0.5% picric acid for ten seconds to differentiate and dehydrate tissue.

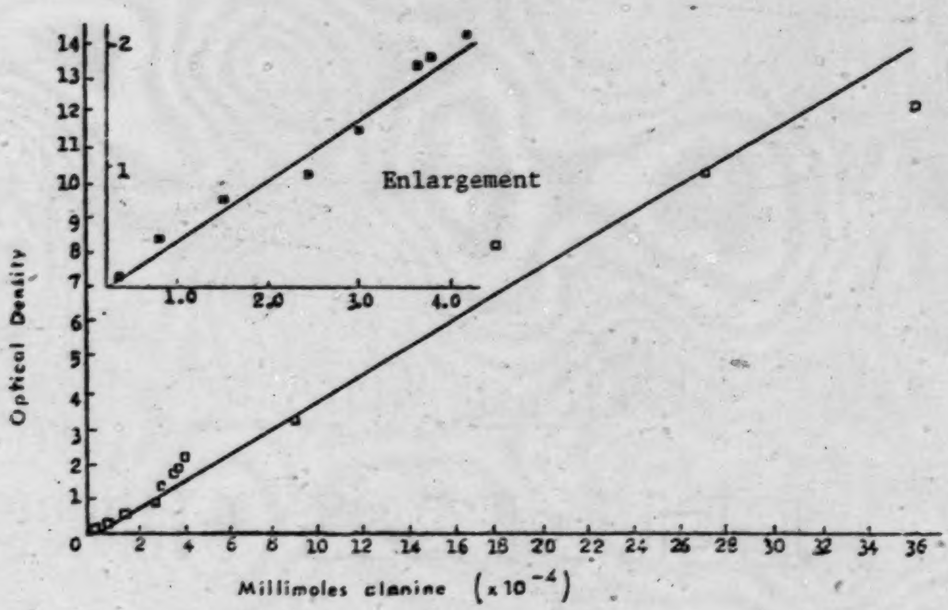
3. The previous treatment was neutralized by transferring slides briefly to ammonified 95% ethanol (4 - 5 drops ammonium hydroxide to 100 ml ethanol).

4. Slides were dehydrated by transfer to absolute ethanol and then counterstained for ten seconds in fast green dye. Fast green solution prepared as follows: fast green dye added to a 1:1 mixture of methyl cellusolve and absolute ethanol to near saturation. This mixture was then added to an equal proportion of a second mixture consisting of twenty-five parts of absolute ethanol and seventy-five parts clove oil.

5. Slides were cleared for two minutes in a solution consisting of fifty parts clove oil, twenty-five parts absolute ethanol, and twenty-five parts xylene.

6. Slides were then transferred to xylene in preparation for mounting.

APPENDIX 5. Standard curve of alanine concentration (millimoles) versus optical density used in determining α - amino nitrogen of leaves by the ninhydrin test.



APPENDIX 6. Data used in plotting graphs of chlorophyll (mg cm^{-2} leaf tissue) and anthocyanin (μg cm^{-2} leaf tissue) content in senescing leaves of E. alata Sieb. 'Compacta'. Optical densities based on a 50 ml extract from which anthocyanin values were calculated are included.

Figure 11. Decline in chlorophyll content of leaves of EG E. alata Sieb. 'Compacta' exposed to modified (11-1) and noncontrolled (11-2) field temperatures from September 17 to November 8, 1976.

11-1 Noncontrolled field temperature treatment.

Date	Chlorophyll concentration (mg cm^{-2})		
	a	b	Total
Sept 17	0.0915 ± .0091	0.0355 ± .0013	0.1290 ± .0099
28	0.0900 ± .0117	0.0302 ± .0055	0.1213 ± .0172
Oct 3	0.0957 ± .0176	0.0299 ± .0026	0.1255 ± .0200
6	0.0915 ± .0084	0.0343 ± .0025	0.1257 ± .0090
14	0.0681 ± .0105	0.0032 ± .0048	0.1004 ± .0150
17	0.0560 ± .0040	0.0033 ± .0018	0.0903 ± .0043
27	0.0606 ± .0061	0.0249 ± .0028	0.0855 ± .0087
Nov 1	0.0435 ± .0089	0.0272 ± .0039	0.0690 ± .0138
8	0.0434 ± .0083	0.0241 ± .0054	0.0679 ± .0132

11-2 Modified field temperature treatment.

Date	Chlorophyll concentration (mg cm^{-2})		
	a	b	Total
Sept 17	0.0915 ± .0041	0.0355 ± .0013	0.1290 ± .0099
23	0.0891 ± .0040	0.0295 ± .0026	0.1186 ± .0038
28	0.0802 ± .0102	0.0308 ± .0044	0.1109 ± .0143
Oct 3	0.0902 ± .0121	0.0313 ± .0023	0.1208 ± .0136
6	0.0816 ± .0080	0.0243 ± .0022	0.1060 ± .0087
14	0.0667 ± .0048	0.0276 ± .0013	0.0941 ± .0060
17	0.0495 ± .0050	0.0317 ± .0023	0.0811 ± .0072
27	0.0406 ± .0042	0.0182 ± .0014	0.0588 ± .0049
Nov 1	0.0226 ± .0037	0.0145 ± .0011	0.0372 ± .0037
8	0.0129 ± .0043	0.0051 ± .0007	0.0141 ± .0026

Figure 12. Increase in anthocyanin content in leaves of EG *E. alata* Sieb 'Compacta' exposed to modified (12-1) and noncontrolled (12-2) field temperatures from September 17 to November 8, 1976.

12-1 Noncontrolled field temperature treatment.

Date	Anthocyanin Concentration	
	Absorbance cm^{-2}	µg cy-3-rh glu cm^{-2}
Sept 17	0.0055 ± .0019	6.3435 ± 2.1914
28	0.0135 ± .0037	15.5705 ± 4.4981
Oct 3	0.0108 ± .0038	12.4564 ± 4.3828
6	0.0154 ± .0043	17.7619 ± 4.9595
14	0.0183 ± .0077	21.1067 ± 8.8809
17	0.0259 ± .0048	29.8723 ± 5.5362
27	0.0290 ± .0051	33.4477 ± 5.8822
Nov 1	0.0427 ± .0054	49.2489 ± 6.2282
8	0.0401 ± .0062	46.2501 ± 7.1509

12.2 Modified field temperature treatment.

Date	Anthocyanin Concentration	
	Absorbance cm^{-2}	µg cy-3-rh glu cm^{-2}
Sept 17	0.0055 ± .0019	6.3435 ± 2.1914
28	0.0100 ± .0026	11.5337 ± 2.9988
Oct 3	0.0106 ± .0021	12.2257 ± 2.4221
6	0.0133 ± .0057	15.3398 ± 6.5742
14	0.0119 ± .0029	13.7251 ± 3.3447
17	0.0127 ± .0022	14.6477 ± 2.5374
27	0.0324 ± .0076	37.3692 ± 8.7656
Nov 1	0.0421 ± .0051	48.5568 ± 5.8822
8	0.0454 ± .0096	52.3629 ± 11.0722

Figure 17. Concentration of chlorophyll (17-1) and anthocyanin (17-2) in leaves of EG potted E. alata Sieb. 'Compacta' exposed to temperatures of 15°C/2°C and a 13 hour photoperiod.

17-1. Chlorophyll content

Days since treatment start	Chlorophyll Concentration (mg cm^{-2})		
	a	b	Total
7	0.0722 ± 0.0158	0.0253 ± 0.0060	0.0975 ± 0.0193
15	0.0679 ± 0.0108	0.0241 ± 0.0048	0.0920 ± 0.0114
25	0.0531 ± 0.0072	0.0249 ± 0.0038	0.0821 ± 0.0109
33	0.0214 ± 0.0075	0.0146 ± 0.0100	0.0302 ± 0.0059
40	0.0166 ± 0.0020	0.0095 ± 0.0013	0.0262 ± 0.0031
47	0.0094 ± 0.0014	0.0045 ± 0.0007	0.0142 ± 0.0021

17-2. Anthocyanin Content.

Days since treatment start	Anthocyanin Concentration	
	Absorbance cm^{-2}	μg cy-3-rh glu cm^{-2}
15	0.0040 ± 0.0003	4.6134 ± 0.3460
25	0.0135 ± 0.0012	15.5702 ± 1.3840
33	0.0212 ± 0.0022	24.4510 ± 2.5374
40	0.0258 ± 0.0028	29.7564 ± 3.2294
47	0.0287 ± 0.0018	33.1264 ± 2.0122

Figure 18. Concentration of chlorophyll (18-1) and anthocyanin (18-2) in leaves of EG potted E. alata Sieb. 'Compacta' exposed to simulated Eastern conditions (15°C/5°C, 13 hour photoperiod).

18-1. Chlorophyll Content.

Days since treatment start	Chlorophyll Concentration (mg cm^{-2})		
	a	b	Total
1	0.0662 ± 0.0066	0.0335 ± 0.0031	0.0994 ± 0.0113
13	0.0605 ± 0.0070	0.0256 ± 0.0025	0.0834 ± 0.0066
17	0.0537 ± 0.0.25	0.0218 ± 0.0036	0.0720 ± 0.0103
23	0.0556 ± 0.0151	0.0241 ± 0.0051	0.0797 ± 0.0191
31	0.0309 ± 0.0047	0.0161 ± 0.0029	0.0470 ± 0.0076
33	0.0092 ± 0.0022	0.0055 ± 0.0017	0.0155 ± 0.0052
38	0.0058 ± 0.0006	0.0025 ± 0.0005	0.0083 ± 0.0010
42	0.0025 ± 0.0010	0.0012 ± 0.0004	0.0037 ± 0.0014

18-2. Anthocyanin content.

Days since treatment start	Anthocyanin Concentration	
	Absorbance cm^{-2}	µg cy-3-rh glu cm^{-2}
13	0.0057 ± 0.0002	6.5721 ± 0.2306
17	0.0071 ± 0.0009	8.1863 ± 1.0377
23	0.0114 ± 0.0009	13.1442 ± 1.0377
31	0.0252 ± 0.0021	29.0556 ± 2.4213
38	0.0350 ± 0.0027	40.3550 ± 3.1130
43	0.0442 ± 0.0018	51.0021 ± 2.1214

Figure 19. Concentration of chlorophyll in leaves of EG *E. alta* Sieb. 'Compacta' exposed to 18°C/10°C and a 13 hour photoperiod.

Days since treatment start	Chlorophyll concentration (mg cm^{-2})		
	a	b	Total
7	0.0662 ± 0.0066	0.0335 ± 0.0031	0.0994 ± 0.0113
15	0.0725 ± 0.0100	0.0340 ± 0.0040	0.1049 ± 0.0151
25	0.0659 ± 0.0063	0.0332 ± 0.0031	0.0990 ± 0.0103
33	0.0539 ± 0.0039	0.0315 ± 0.0038	0.0896 ± 0.0120
40	0.0722 ± 0.0075	0.0253 ± 0.0060	0.0973 ± 0.0081

Figure 20. Concentration of chlorophyll (20-1) and anthocyanin (20-2) in leaves of EG *E. alata* Sieb. 'Compacta' exposed to simulated Western conditions (15°C/2°C, then 15°C/0°C/-5°C and a 13 hour photoperiod).

20-1. Chlorophyll content.

Days since treatment start	Chlorophyll concentration (mg cm^{-2})		
	a	b	Total
1	0.0659 ± 0.0063	0.0332 ± 0.0031	0.0991 ± 0.0092
13	0.0725 ± 0.0100	0.0360 ± 0.0042	0.1085 ± 0.0141
17	0.0528 ± 0.0080	0.0302 ± 0.0022	0.0830 ± 0.0100
21	0.0632 ± 0.0079	0.0325 ± 0.0030	0.0957 ± 0.0105
30	0.0344 ± 0.0040	0.0179 ± 0.0024	0.0523 ± 0.0063
38	0.0245 ± 0.0027	0.0136 ± 0.0016	0.0380 ± 0.0042
43	0.0102 ± 0.0022	0.0070 ± 0.0013	0.0173 ± 0.0034
48	0.0129 ± 0.0012	0.0076 ± 0.0006	0.0206 ± 0.0018

20-2. Anthocyanin Content.

Days since treatment start	Anthocyanin Concentration	
	Absorbance cm^{-2}	μg cy-3-rh glu cm^{-2}
23	0.0023 ± 0.0003	2.6519 ± 0.3459
30	0.0082 ± 0.0007	9.4546 ± 0.8071
38	0.0154 ± 0.0077	17.7562 ± 8.8781
43	0.0222 ± 0.0014	25.5966 ± 1.6142
48	0.0317 ± 0.0057	36.5501 ± 6.5721

Figure 21. Decline in chlorophyll content in leaves of EG *E. alata* Sieb. 'Compacta' exposed to temperatures of 15 C/2 C and a photoperiod of 13 hours (21-1) or 18 hours(21-2).

21-1. 13 hour photoperiod.

Days since treatment start	Chlorophyll concentration (mg cm^{-2})		
	a	b	Total
7	0.0722 ± 0.0158	0.0253 ± 0.0060	0.0975 ± 0.0195
15	0.0679 ± 0.0108	0.0241 ± 0.0048	0.0920 ± 0.0114
25	0.0531 ± 0.0072	0.0299 ± 0.0038	0.0821 ± 0.0100
33	0.0214 ± 0.0075	0.0146 ± 0.0100	0.0302 ± 0.0059
40	0.0166 ± 0.0050	0.0095 ± 0.0013	0.0262 ± 0.0031
47	0.0094 ± 0.0014	0.0045 ± 0.0007	0.0142 ± 0.0021

21-2. 18 hour photoperiod.

Days since treatment start	Chlorophyll concentration (mg cm^{-2})		
	a	b	Total
1	0.0900 ± .0079	0.0300 ± .0012	0.1199 ± .0088
4	0.0899 ± .0033	0.0270 ± .0045	0.1169 ± .0071
8	0.0784 ± .0157	0.0225 ± .0057	0.1009 ± .0214
10	0.0672 ± .0033	0.0235 ± .0013	0.0912 ± .0026
16	0.0677 ± .0058	0.0240 ± .0042	0.0917 ± .0093
20	0.0620 ± .0076	0.0211 ± .0015	0.0831 ± .0090
25	0.0702 ± .0075	0.0202 ± .0010	0.0903 ± .0081
31	0.0703 ± .0059	0.0225 ± .0065	0.0872 ± .0168
36	0.0643 ± .0129	0.0238 ± .0026	0.0881 ± .0154
41	0.0624 ± .0063	0.0220 ± .0022	0.0844 ± .0083
46	0.0742 ± .0066	0.0245 ± .0006	0.0984 ± .0067
64	0.0185 ± .0056	0.0085 ± .0016	0.0270 ± .0070
71	0.0107 ± .0018	0.0063 ± .0007	0.0169 ± .0015

Figure 22. Increase in anthocyanin content in leaves of EG *E. alata* Sieb. 'Compacta' exposed to temperatures of 15°C/2°C and a photoperiod of 13 hours (22-1) and 18 hours (22-2).

22-1. 13 hour photoperiod.

Days since treatment start	Anthocyanin concentration	
	Absorbance cm^{-2}	ug cy-3-rh glu cm^{-2}
15	0.0040 ± 0.0003	4.6134 ± 0.3460
25	0.0135 ± 0.0012	15.5702 ± 1.3840
33	0.0212 ± 0.0022	24.4510 ± 2.5374
40	0.0258 ± 0.0028	29.7564 ± 3.2294
47	0.0287 ± 0.0018	33.1264 ± 2.0122

22-3. 18 hour photoperiod.

Days since treatment start	Anthocyanin concentration	
	Absorbance cm^{-2}	ug cy-3-rh glu cm^{-2}
12	0.0033 ± .0012	3.8049 ± 1.3836
16	0.0018 ± .0007	2.0754 ± 0.8071
20	0.0019 ± .0007	2.1907 ± 0.8071
25	0.0017 ± .0007	1.9601 ± 0.8071
31	0.0053 ± .0009	6.1109 ± 1.0377
36	0.0078 ± .0003	8.9934 ± 0.3460
41	0.0124 ± .0019	14.2972 ± 2.1908
46	0.0153 ± .0004	17.6409 ± 0.4612
64	0.0435 ± .0016	50.1555 ± 1.8448
71	0.0671 ± .0011	77.3663 ± 1.2683

Figure 23. Decline in chlorophyll content in leaves of EG E. alata Sieb. 'Compacta' exposed to Western (18 hours for 2 weeks, then 13 hours) 23-1 and Eastern (13 hours) photoperiod 23-2 . Temperatures held constant at 15 C/2 C.

23-1. Western photoperiod treatment.

Days since treatment start	Chlorophyll Concentration (mg cm^{-2}) a	b	Total
4	0.0527 ± .0056	0.0192 ± .0004	0.0719 ± .0060
13	0.0641 ± .0030	0.0236 ± .0015	0.0857 ± .0064
19	0.0492 ± .0078	0.0195 ± .0018	0.0689 ± .0095
26	0.0471 ± .0037	0.0186 ± .0011	0.0657 ± .0046
33	0.0470 ± .0062	0.0134 ± .0030	0.0604 ± .0041
40	0.0404 ± .0032	0.0141 ± .0006	0.0545 ± .0035
49	0.0373 ± .0068	0.0222 ± .0033	0.0594 ± .0100
61	0.0240 ± .0024	0.0102 ± .0006	0.0342 ± .0024
72	0.0186 ± .0014	0.0074 ± .0006	0.0260 ± .0030
87	0.0087 ± .0012	0.0038 ± .0006	0.0125 ± .0017
97	0.0078 ± .0014	0.0035 ± .0011	0.0105 ± .0018
104	0.0086 ± .0012	0.0037 ± .0006	0.0123 ± .0017

23-2. Eastern photoperiod treatment.

Days since treatment start	Chlorophyll Concentration (mg cm^{-2}) a	b	Total
4	0.0535 ± .0059	0.0198 ± .0003	0.0733 ± 0.0062
13	0.0491 ± .0032	0.0190 ± .0008	0.0681 ± 0.0038
19	0.0508 ± .0088	0.0197 ± .0023	0.0705 ± 0.0114
26	0.0485 ± .0036	0.0198 ± .0018	0.0683 ± 0.0046
33	0.0468 ± .0062	0.0127 ± .0031	0.0595 ± 0.0042
40	0.0415 ± .0033	0.0153 ± .0011	0.0568 ± 0.0034
49	0.0359 ± .0069	0.0208 ± .0033	0.0568 ± 0.0101
61	0.0248 ± .0026	0.0109 ± .0006	0.0357 ± 0.0311
72	0.0187 ± .0079	0.0077 ± .0012	0.0356 ± 0.0122
78	0.0187 ± .0014	0.0074 ± .0006	0.0261 ± 0.0197

Figure 24. Increase in anthocyanin content in leaves of EG *E. alata* Sieb. 'Compacta' exposed to Western (18 hours for 2 weeks, then 13 hours) 24-1 or Eastern (13 hours) photoperiod. 24-2 Temperatures held constant at 15°C/2°C.

24-1. Western photoperiod treatment.

Days since treatment start	Anthocyanin Concentration	
	Absorbance cm^{-2}	µg cy-3-rh glu cm^{-2}
33	0.0116 ± .0037	13.3594 ± 4.2768
40	0.0207 ± .0040	23.8402 ± 4.6457
49	0.0248 ± .0041	28.5716 ± 4.7736
61	0.0331 ± .0048	38.2084 ± 5.5841
72	0.0378 ± .0021	43.6312 ± 2.4668
87	0.0445 ± .0073	51.3756 ± 8.4454
97	0.0543 ± .0131	57.9203 ± 10.7656
104	0.0524 ± .0063	60.3914 ± 7.2456

24-2. Eastern photoperiod treatment.

Days since treatment start	Anthocyanin Concentration	
	Absorbance cm^{-2}	µg cy-3-rh glu cm^{-2}
33	0.0113 ± .0039	13.1239 ± 4.4806
40	0.0198 ± .0029	22.8049 ± 3.3259
49	0.0257 ± .0024	29.6501 ± 2.7676
61	0.0337 ± .0034	38.8367 ± 3.8641
72	0.0348 ± .0039	40.2095 ± 4.4661
78	0.0569 ± .0068	65.6408 ± 7.8408

Figure 25. Decline in chlorophyll content in leaves of EG *E. alata* Sieb. 'Compacta' exposed to temperatures of 15°C/2°C, a 13 hour photoperiod and a far-red:red light ratio of 1.7 (25-1) and less than 0.5 (25-2).

25-1. Far-red:red light ratio - 1.7.

Days since treatment start	Chlorophyll concentration (mg cm^{-2})		
	a	b	Total
1	0.0247 ± 0.0067	0.0115 ± 0.0037	0.0363 ± 0.0103
5	0.0297 ± 0.0099	0.0136 ± 0.0018	0.0433 ± 0.0058
11	0.0272 ± 0.0020	0.0135 ± 0.0012	0.0365 ± 0.0034
19	0.0208 ± 0.0018	0.0105 ± 0.0014	0.0308 ± 0.0029
26	0.0215 ± 0.0031	0.0088 ± 0.0015	0.0303 ± 0.0044
33	0.0166 ± 0.0021	0.0086 ± 0.0013	0.0252 ± 0.0030
42	0.0116 ± 0.0012	0.0083 ± 0.0005	0.0200 ± 0.0010
54	0.0091 ± 0.0024	0.0044 ± 0.0013	0.0135 ± 0.0035
65	0.0059 ± 0.0027	0.0027 ± 0.0015	0.0086 ± 0.0042

25-2. Far-red:red light ratio - less than 0.5

Days since treatment start	Chlorophyll Concentration (mg cm^{-2})		
	a	b	Total
7	0.0722 ± 0.0158	0.0253 ± 0.0060	0.0975 ± 0.0101
15	0.0679 ± 0.0108	0.0241 ± 0.0048	0.0920 ± 0.0110
25	0.0531 ± 0.0072	0.0299 ± 0.0038	0.0821 ± 0.0100
33	0.0214 ± 0.0075	0.0146 ± 0.0100	0.0302 ± 0.0052
40	0.0166 ± 0.0020	0.0095 ± 0.0013	0.0262 ± 0.0031
47	0.0094 ± 0.0014	0.0045 ± 0.0007	0.0142 ± 0.0022

Figure 26. Increase in anthocyanin content in leaves of EG *E. alata* Sieb. 'Compacta' exposed to temperatures of 15°C/2°C and a 13 hour photoperiod. Far-red:red light ratios 1.7 (26-1), and less than 0.5 (26-2).

26-1. Far-red:red light ratio - 1.7.

Days since treatment start	Anthocyanin Concentration	
	Absorbance cm^{-2}	µg cy-3-rh glu cm^{-2}
26	0.0100 ± 0.0006	11.5372 ± 0.7848
33	0.0088 ± 0.0015	10.0990 ± 1.7201
42	0.0167 ± 0.0024	19.2560 ± 2.7845
54	0.0241 ± 0.0039	27.8195 ± 4.4734
65	0.0448 ± 0.0044	51.6832 ± 5.0201

26-2. Far-red:red light ratio - less than 0.5

Days since treatment start	Anthocyanin Concentration	
	Absorbance cm^{-2}	µg cy-3-rh glu cm^{-2}
15	0.0040 ± 0.0003	4.6134 ± 0.3460
25	0.0135 ± 0.0012	15.5702 ± 1.3840
33	0.0212 ± 0.0022	24.4510 ± 2.5374
40	0.0258 ± 0.0028	29.7564 ± 3.2294
47	0.0287 ± 0.0018	33.1264 ± 2.0122

Figure 27. Decline in chlorophyll content in leaves of (27-1) WG and (27-2) EG *E. alata* Sieb. 'Compacta' in the field, September 17 to November 8, 1976.

27-1. WG Plants

Date	Chlorophyll Concentration (mg cm^{-2})		
	a	b	Total
Sept 28	0.0922 ± .0049	0.0284 ± .0015	0.1205 ± .0060
Oct 3	0.0777 ± .0063	0.0247 ± .0021	0.1024 ± .0069
6	0.1010 ± .0119	0.0311 ± .0036	0.1321 ± .0127
14	0.0395 ± .0073	0.0164 ± .0030	0.0558 ± .0098
17	0.0532 ± .0052	0.0333 ± .0035	0.0865 ± .0087
27	0.0285 ± .0034	0.0132 ± .0018	0.0416 ± .0048

27-2. EG Plants

Date	Chlorophyll Concentration (mg cm^{-2})		
	a	b	Total
Sept 17	0.0915 ± .0091	0.0355 ± .0013	0.1290 ± .0061
28	0.0900 ± .0043	0.0302 ± .0055	0.1213 ± .0170
Oct 3	0.0957 ± .0176	0.0299 ± .0026	0.1235 ± .0200
6	0.0915 ± .0084	0.0343 ± .0025	0.1257 ± .0090
14	0.0681 ± .0105	0.0324 ± .0048	0.1004 ± .0150
17	0.0560 ± .0040	0.0336 ± .0018	0.0903 ± .0043
27	0.0606 ± .0061	0.0249 ± .0028	0.0855 ± .0087
Nov 1	0.0435 ± .0089	0.0272 ± .0039	0.0690 ± .0132
8	0.0434 ± .0083	0.0241 ± .0054	0.0679 ± .0132

Figure 28. Increase in anthocyanin content in leaves of (28-1) WG and (28-2) EG *E. alata* Sieb. 'Compacta' in the field, September 17 to November 8, 1976.

28-1. WG Plants

Date	Anthocyanin Concentration	
	Absorbance cm^{-2}	µg cy-3-rh glu cm^{-2}
Sept 28	0.0138 ± .0036	15.9165 ± 4.1521
Oct 3	0.0137 ± .0047	15.8012 ± 5.4208
6	0.0149 ± .0034	17.1852 ± 3.9215
14	0.0343 ± .0047	39.5606 ± 5.4208
17	0.0246 ± .0082	28.3709 ± 9.4576
27	0.0358 ± .0088	41.2906 ± 10.1497

28-2. EG Plants

Date	Anthocyanin Concentration Absorbance cm^{-2}	 µg cy-3-rh glu cm^{-2}
Sept 17	0.0055 ± .0019	6.3435 ± 2.1914
28	0.0135 ± .0037	15.5705 ± 4.4981
Oct 3	0.0108 ± .0038	12.4564 ± 4.3828
6	0.0154 ± .0043	17.7619 ± 4.9595
14	0.0183 ± .0077	21.1067 ± 8.8809
17	0.0259 ± .0048	29.8723 ± 5.5362
27	0.0290 ± .0051	33.4477 ± 5.8822
Nov 1	0.0427 ± .0054	49.2489 ± 6.2282
8	0.0401 ± .0062	46.2501 ± 7.1509

Figure 29. Decline in chlorophyll content in leaves of cuttings taken from (29-1) WG and (29-2) EG *E. alata* Sieb. 'Compacta' plants exposed to temperatures of 15°C/2°C and a 13 hour photoperiod.

29-1. Cuttings taken from WG Plants

Days since treatment start	Chlorophyll Concentration a	 b	 Total
3	0.0982 ± 0.0087	0.0646 ± 0.0076	0.1617 ± 0.0155
9	0.0953 ± 0.0030	0.0507 ± 0.0032	0.1462 ± 0.0061
19	0.0854 ± 0.0075	0.0431 ± 0.0030	0.1285 ± 0.0103
24	0.0884 ± 0.0034	0.0449 ± 0.0016	0.1333 ± 0.0035
29	0.0803 ± 0.0064	0.0424 ± 0.0027	0.1228 ± 0.0081
41	0.0881 ± 0.0028	0.0451 ± 0.0024	0.1338 ± 0.0045
48	0.0853 ± 0.0104	0.0416 ± 0.0033	0.1267 ± 0.0133

29-2. Cuttings taken from EG Plants

Days since treatment start	Chlorophyll Concentration a	 b	 Total
2	0.0525 ± 0.0056	0.0327 ± 0.0028	0.0851 ± 0.0058
9	0.0537 ± 0.0037	0.0313 ± 0.0035	0.0870 ± 0.0056
19	0.0546 ± 0.0067	0.0356 ± 0.0154	0.0902 ± 0.0163
24	0.0595 ± 0.0089	0.0281 ± 0.0040	0.0841 ± 0.0092
29	0.0343 ± 0.0036	0.0186 ± 0.0026	0.0526 ± 0.0058

Figure 30. Decline in chlorophyll content in leaves of EG *E. alata* Sieb. 'Compacta' formed under (30-1) 20°C/7°C, 16 hour photoperiod, (30-2) 23°C/13°C, 16 hour photoperiod and (30-3) 20°C/7°C, 18 hour photoperiod.

30-1. 20°C/7°C, 16 hour photoperiod.

Days since treatment start	Chlorophyll Concentration (mg cm $^{-2}$)		
	a	b	Total
4	0.0352 ± .0055	0.0151 ± .0021	0.0503 ± .0072
13	0.0556 ± .0057	0.0191 ± .0013	0.0747 ± .0069
19	0.0568 ± .0103	0.0215 ± .0015	0.0780 ± .0119
26	0.0620 ± .0050	0.0191 ± .0029	0.0811 ± .0070
33	0.0519 ± .0084	0.0178 ± .0036	0.0697 ± .0111
40	0.0492 ± .0067	0.0158 ± .0032	0.0651 ± .0098
49	0.0482 ± .0088	0.0286 ± .0039	0.0778 ± .0116
61	0.0259 ± .0044	0.0101 ± .0017	0.0360 ± .0061
72	0.0101 ± .0017	0.0042 ± .0009	0.0143 ± .0025
79	0.0047 ± .0006	0.0018 ± .0006	0.0068 ± .0010

30-2. 23°C/13°C, 16 hour photoperiod.

Days since treatment start	Chlorophyll Concentration (mg cm $^{-2}$)		
	a	b	Total
4	0.0427 ± 0.0039	0.0184 ± 0.0018	0.0611 ± 0.0055
13	0.0548 ± 0.0060	0.0227 ± 0.0033	0.0775 ± 0.0079
19	0.0615 ± 0.0041	0.0231 ± 0.0018	0.0843 ± 0.0062
26	0.0450 ± 0.0065	0.0158 ± 0.0013	0.0607 ± 0.0077
33	0.0436 ± 0.0027	0.0157 ± 0.0014	0.0593 ± 0.0011
40	0.0517 ± 0.0066	0.0180 ± 0.0025	0.0697 ± 0.0089
49	0.0441 ± 0.0036	0.0256 ± 0.0026	0.0691 ± 0.0066
61	0.0129 ± 0.0010	0.0061 ± 0.0007	0.0190 ± 0.0015
72	0.0141 ± 0.0014	0.0064 ± 0.0008	0.0205 ± 0.0019
87	0.0047 ± 0.0005	0.0021 ± 0.0003	0.0069 ± 0.0006

30-3. 20°C/7°C, 18 hour photoperiod.

Days since treatment start	Chlorophyll Concentration (mg cm $^{-2}$)		
	a	b	Total
4	0.0535 ± .0059	0.0198 ± .0003	0.0733 ± 0.0062
13	0.0491 ± .0032	0.0196 ± .0008	0.0681 ± 0.0038
19	0.0508 ± .0088	0.0197 ± .0023	0.0705 ± 0.0114
26	0.0485 ± .0036	0.0198 ± .0018	0.0683 ± 0.0046
33	0.0468 ± .0062	0.0127 ± .0031	0.0595 ± 0.0042
40	0.0415 ± .0033	0.0153 ± .0011	0.0568 ± 0.0101
49	0.0359 ± .0069	0.0208 ± .0033	0.0568 ± 0.0101
61	0.0248 ± .0026	0.0109 ± .0006	0.0357 ± 0.0311
72	0.0187 ± .0079	0.0077 ± .0012	0.0356 ± 0.0122
78	0.0187 ± .0014	0.0074 ± .0006	0.0261 ± 0.0197

Figure 31. Increase in anthocyanin content in leaves of EG E. alata Sieb. 'Compacta' fomred under (31-1) 20°C/7°C, 16 hour photoperiod, (31-2) 23°C/13°C, 16 hour photoperiod, and (30-3) 20°C/7°C, 18 hour photoperiod.

31-1. 20°C/7°C, 16 hour photoperiod.

Days since treatment since	Anthocyanin Concentration	
	Absorbance cm $^{-2}$	µg cy-3-rh glu cm $^{-2}$
33	.0037 ± .0014	4.3178 ± 1.6495
40	.0100 ± .0039	11.5112 ± 4.4962
19	.0084 ± .0020	9.6870 ± 2.3150
61	.0184 ± .0028	21.2584 ± 3.2497
72	.0278 ± .0022	32.0920 ± 2.5781
79	.0321 ± .0040	37.0694 ± 4.5969

31-2. 23°C/13°C. 16 hour photoperiod.

Days since treatment since	Anthocyanin Concentration	
	Absorbance cm $^{-2}$	µg cy-3-rh glu cm $^{-2}$
33	.0018 ± .0002	2.1300 ± .1000
40	.0046 ± .0009	5.3014 ± .4482
49	.0054 ± .0003	6.2436 ± .1584
61	.0129 ± .0025	14.0288 ± 1.2757
72	.0213 ± .0029	24.6148 ± 1.5074
87	.0307 ± .0115	35.3993 ± 2.2115

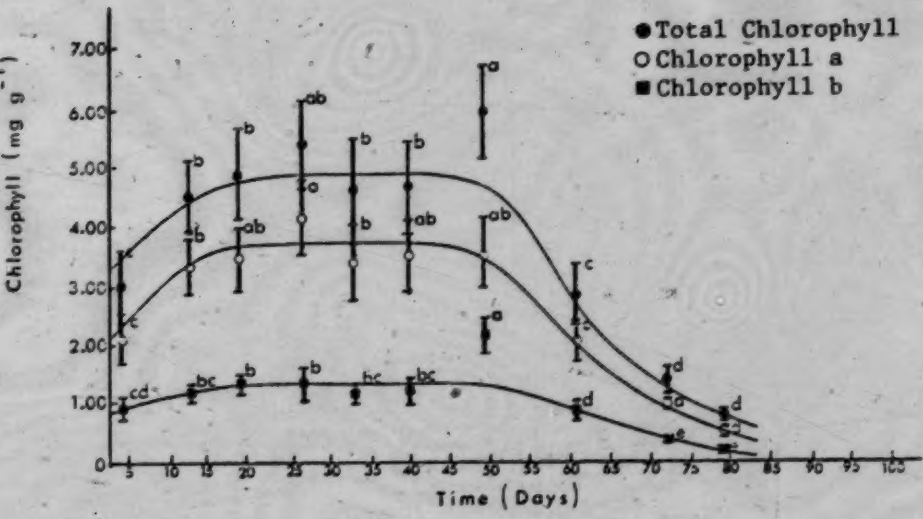
31-3. 20°C/7°C, 18 hour photoperiod.

Days since treatment start	Anthocyanin Concentration Absorbance cm $^{-2}$	µg cy-3-rh glu cm $^{-2}$
33	0.0113 ± .0039	13.1239 ± 4.4806
40	0.0198 ± .0029	22.8049 ± 3.3259
49	0.0257 ± .0024	29.6521 ± 2.7676
61	0.0337 ± .0034	38.8367 ± 3.8641
72	0.0348 ± .0039	40.2095 ± 4.4661
78	0.0569 ± .0068	65.6408 ± 7.8408

Appendix 7. Changes in chlorophyll and anthocyanin content, expressed on the basis of leaf tissue weight (mg g $^{-1}$), in leaves of E. alata Sieb. 'Compacta' grown for one season under various combinations of temperature and photoperiod. Temperatures and photoperiod used to induce senescence, 15°C/2°C and 13 hours, respectively.

A. Western temperatures (20°C/7°C) and Eastern photoperiod (16 hours), PAR-420 $\mu E\ m^{-2}s^{-1}$.

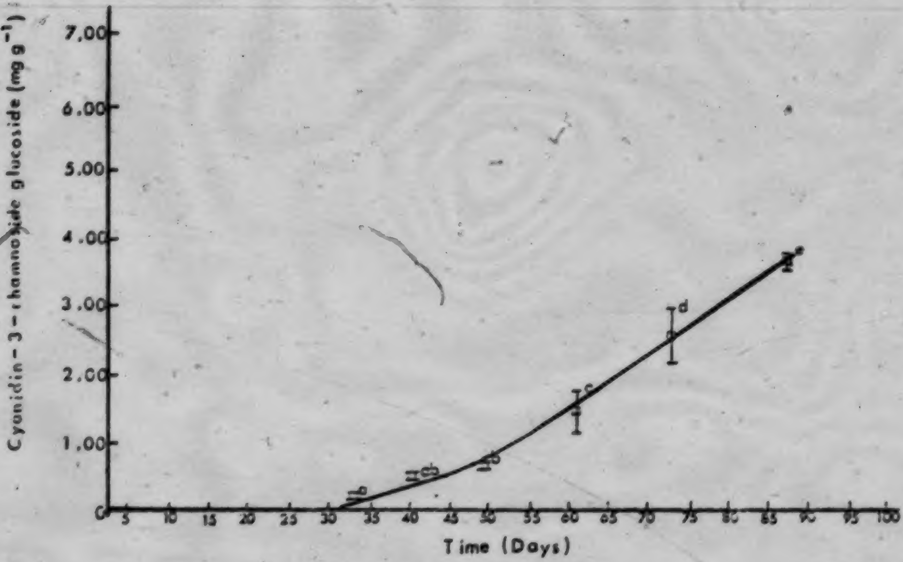
1. Graph - Chlorophyll content



2. Data used in plotting graph

Days since trial start	Chlorophyll Concentration (mg g $^{-1}$)		
	a	b	Total
4	2.1193 ± 0.4401	0.9077 ± 0.1718	3.0262 ± 0.5985
13	3.3397 ± 0.4706	1.1498 ± 0.1271	4.4884 ± 0.5954
19	3.5524 ± 0.6798	1.3131 ± 0.1297	4.9242 ± 0.8096
26	4.1482 ± 0.5709	1.2792 ± 0.2586	5.4272 ± 0.7896
30	3.4308 ± 0.7097	1.1739 ± 0.2784	4.6039 ± 0.9339
40	3.5362 ± 0.5614	1.1387 ± .02486	4.6737 ± 0.8005
49	3.6195 ± 0.6039	2.1388 ± 0.2976	5.8568 ± 0.8094
61	2.0281 ± 0.3378	0.7944 ± 0.1333	2.8219 ± 0.4674
72	0.9673 ± 0.1343	0.4010 ± 0.0713	1.3687 ± 0.1930
79	0.4683 ± 0.1071	0.1979 ± 0.0579	0.6860 ± 0.1927

3. Graph - Anthocyanin Content

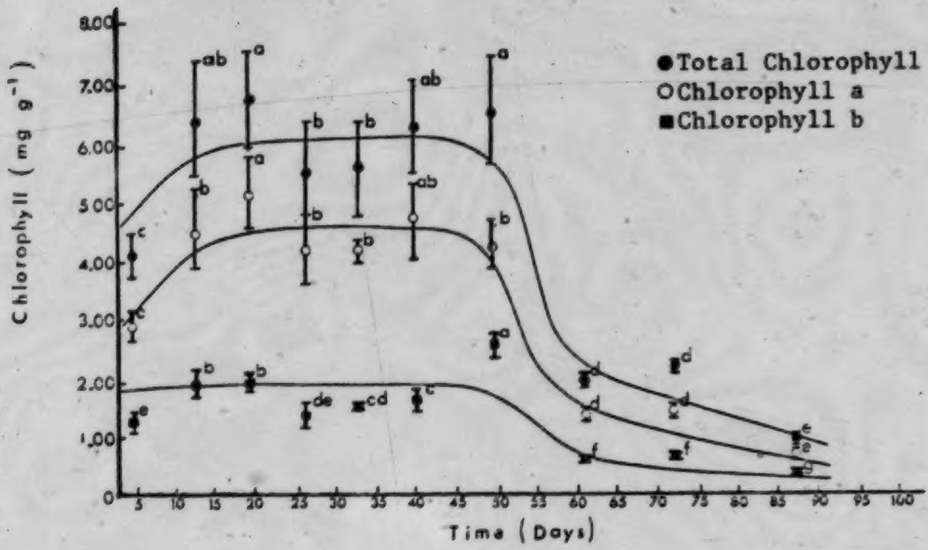


4. Data used in plotting graph

Days since treatment start	Anthocyanin Concentration	
	Absorbance g^{-1}	mg cy-3-rh glu g^{-1}
33	0.1769 ± 0.0259	0.2040 ± 0.0298
40	0.4164 ± 0.0757	0.4802 ± 0.0873
49	0.5223 ± 0.0481	0.5982 ± 0.0547
61	1.3244 ± 0.2829	1.5275 ± 0.3262
72	2.2427 ± 0.3805	2.5868 ± 0.4388
87	3.0966 ± 0.1229	3.5714 ± 0.1418

B. Eastern temperatures (23°C/13°C) and photoperiod (16 hours), PAR-420 $\mu E\ m^{-2} s^{-1}$.

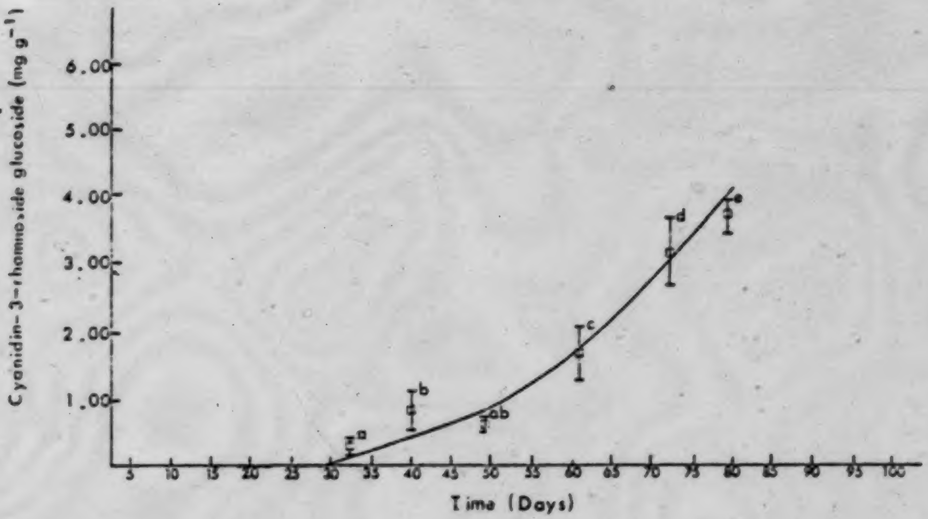
1. Graph - Chlorophyll content



2. Data used in plotting graph

Days since trial start	Chlorophyll Concentration (mg g $^{-1}$)		
	a	b	Total
4	2.8522 ± 0.2401	1.2306 ± 0.1260	4.0818 ± 0.3597
13	4.5470 ± 0.7595	1.8768 ± 0.3052	6.4227 ± 0.9843
19	5.1946 ± 0.6552	1.9275 ± 0.1344	6.8228 ± 0.8253
26	4.1193 ± 0.6398	1.3767 ± 0.1783	5.5749 ± 0.7740
33	4.1528 ± 0.2013	1.4934 ± 0.1083	5.6448 ± 0.3049
40	4.6860 ± 0.5824	1.6326 ± 0.2097	6.3171 ± 0.7737
49	4.2452 ± 0.4005	2.6088 ± 0.2103	6.5765 ± 0.9054
61	1.3115 ± 0.0665	0.6187 ± 0.0561	1.9298 ± 0.1061
72	1.4319 ± 0.0738	0.6496 ± 0.0418	2.0810 ± 0.0501
87	0.5990 ± 0.0851	0.2726 ± 0.0447	0.8514 ± 0.0907

3. Graph - Anthocyanin Content

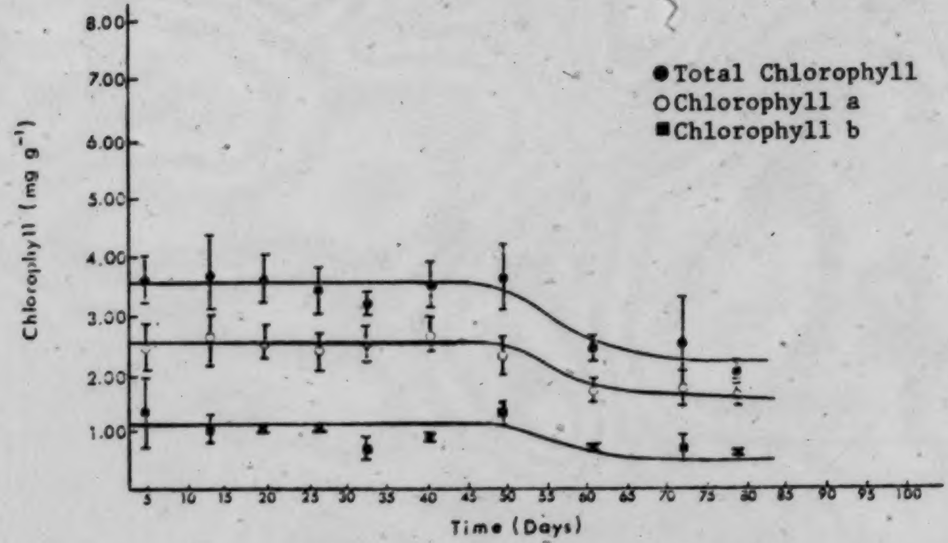


4. Data used in plotting graph

Days since trial start	Anthocyanin Concentration	
	Absorbance g^{-1}	mg cy-3-rh glu g^{-1}
33	0.2404 ± 0.0844	0.2773 ± 0.0974
40	0.7128 ± 0.2702	0.8221 ± 0.3116
49	0.6265 ± 0.1929	0.6226 ± 0.0814
61	1.4539 ± 0.3037	1.6768 ± 0.3503
72	2.2302 ± 1.1224	3.1118 ± 0.4691
79	3.1022 ± 0.2189	3.5779 ± 0.2525

C. Western temperatures (20°C/7°C) and photoperiod (18 hours), PAR-380 $\mu E\ m^{-2} s^{-1}$.

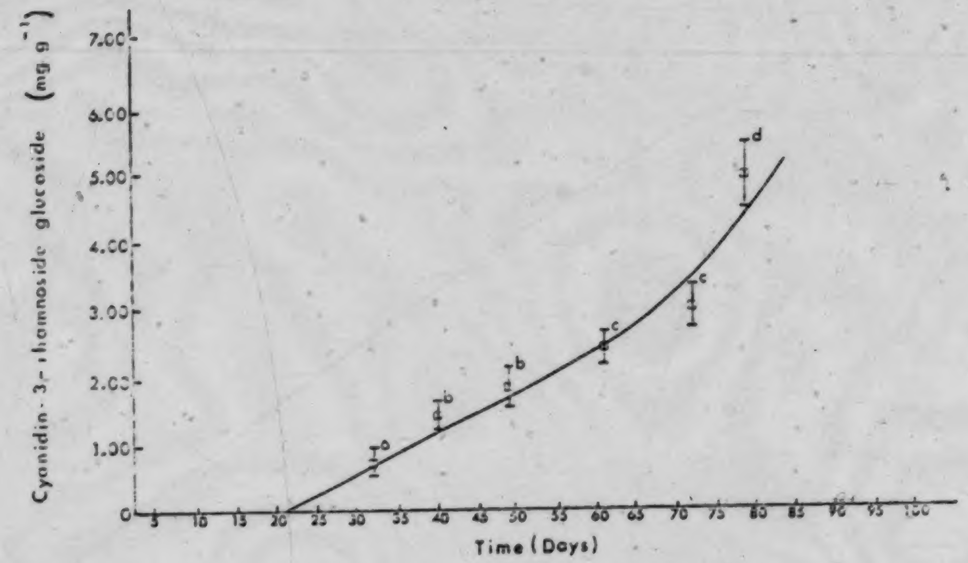
1. Graph - Chlorophyll content



2. Data used in plotting graph

Days since treatment start	Chlorophyll Concentration (mg g $^{-1}$)		
	a	b	Total
4	2.1847 ± 0.4567	1.0334 ± 0.1853	3.2172 ± 0.6296
13	3.3455 ± 0.4360	1.1217 ± 0.1139	4.4661 ± 0.5315
19	3.5264 ± 0.6690	1.3887 ± 0.0722	4.6336 ± 1.0023
26	3.0980 ± 1.7171	1.3131 ± 0.2241	4.7112 ± 0.4001
33	3.4309 ± 0.7077	1.1762 ± 0.2581	4.6059 ± 0.9161
40	3.5470 ± 0.5076	1.1295 ± 0.2430	4.6754 ± 0.7989
49	3.6412 ± 0.9081	2.1566 ± 0.4256	5.7962 ± 1.3234
61	2.0263 ± 0.3411	0.7956 ± 0.1484	2.8212 ± 0.4807
72	1.9798 ± 0.5736	0.7121 ± 0.2143	2.7215 ± 0.2221
82	0.5088 ± 0.1297	0.2115 ± 0.0614	0.7201 ± 0.1897

3. Graph - Anthocyanin content

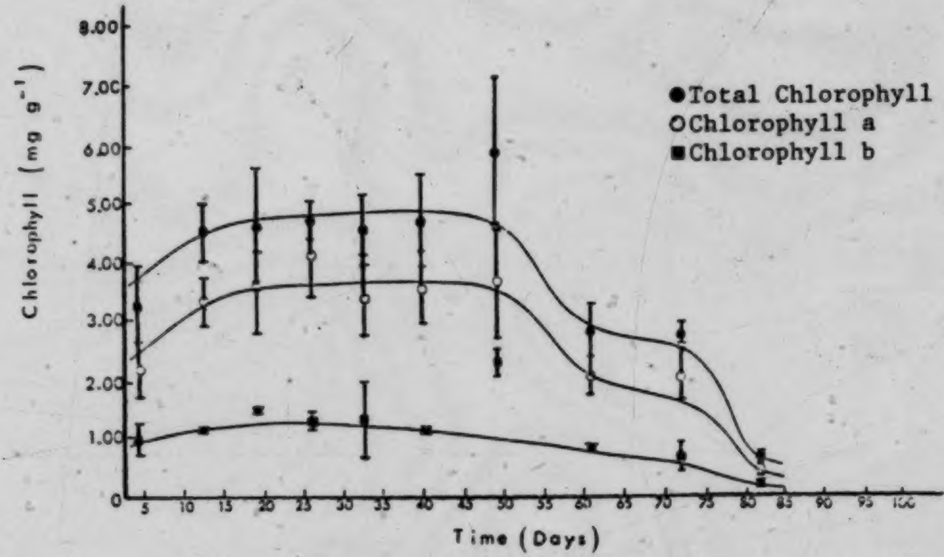


4. Data used in plotting graph

Days since treatment start	Anthocyanin Concentation	
	Absorbance g^{-1}	mg gy-3-rh glu g^{-1}
33	0.0002 ± 0.0003	0.2483 ± 0.0414
40	0.0006 ± 0.0001	0.7103 ± 0.1449
49	0.0006 ± 0.0001	0.6657 ± 0.1333
61	0.0012 ± 0.0003	1.3886 ± 0.3140
72	0.0029 ± 0.0008	3.4271 ± 0.8922
82	0.0030 ± 0.0035	3.4713 ± 0.4129

D. Western temperatures (20°C/7°C) and photoperiod (18 hours), PAR-420 $\mu E\ m^{-2}s^{-1}$.

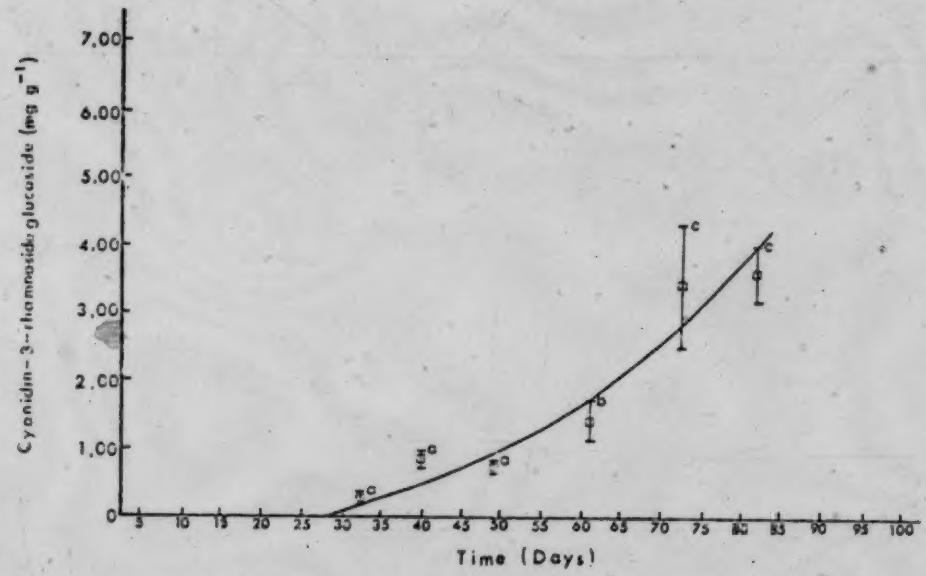
1. Graph - Chlorophyll content



2. Data used in plotting graph

Days since Treatment start	Chlorophyll Concentration (mg g $^{-1}$) a	b	Total
4	2.5084 ± 0.4044	1.2682 ± 0.5974	3.5755 ± 0.3773
13	2.6894 ± 0.5093	1.0375 ± 0.1665	3.7260 ± 0.6730
19	2.5860 ± 0.2760	1.0069 ± 0.1057	3.5920 ± 0.3670
26	2.4378 ± 0.3356	0.9899 ± 0.1007	3.4267 ± 0.4223
33	2.5140 ± 0.3094	0.6835 ± 0.1804	3.1968 ± 0.2492
40	2.5723 ± 0.3192	0.9457 ± 0.0921	3.5177 ± 0.5956
49	2.2565 ± 0.4165	1.3101 ± 0.1958	3.5656 ± 0.6119
61	1.5933 ± 0.1755	0.6993 ± 0.0405	2.2920 ± 0.2101
72	1.6500 ± 0.3138	0.6790 ± 0.1745	2.4884 ± 0.8374
78	1.4026 ± 0.1877	0.5537 ± 0.0750	1.9558 ± 0.2610

3. Graph - Anthocyanin content



4. Data used in plotting graph

Days since treatment start	Anthocyanin Concentration	
	Absorbance g^{-1}	mg cy-3-rh glu g^{-1}
33	0.0006 ± 0.0002	0.6998 ± 0.1899
40	0.0013 ± 0.0002	1.4433 ± 0.2045
49	0.0015 ± 0.0002	1.7613 ± 0.2783
61	0.0022 ± 0.0002	2.4915 ± 0.2509
72	0.0025 ± 0.0003	2.9784 ± 0.3439
78	0.0043 ± 0.0005	4.9823 ± 0.5446

APPENDIX 8. Growth Chamber Specifics

Chamber size

A chamber (Environmental Growth Chambers, Chagrin Falls, Ohio) with inside dimensions of 1.3 m x 2.6 m was used in all controlled environment treatments except Treatment 1 (far-red:red light ratio 1.7) of the light quality experiment (page 50). In this treatment, a chamber with inside dimension of 0.8 x 1.0 m was used. All chambers had a mylar barrier separating the light source from the growing area.

Light

In all treatments where senescence of the plants was induced (except Treatment 1 of the light quality experiment, page 50), light was provided by eight equally spaced cool white fluorescent lamps (Sylvania P96 T10/CW). The higher far-red:red light ratio (1.7) in Treatment 1 of the light quality experiment was provided by six equally spaced cool white fluorescent lamps (Sylvania F48 T12/CW VHO) and four 100 W incandescent lamps.

In treatments where leaf growth was promoted (rather than senesced) under controlled environment conditions, light was provided by 24 equally spaced cool white fluorescent lamps (Sylvania F96T210/CW) and ten 100 W incadenscent lamps.

Light intensities listed for each treatment throughout the Materials and Methods section were measured at the beginning of each experiment. All readings were made at mid-plant height. At the end of each light period in photoperiod treatments the change from light to dark was abrupt.

Temperature

Ambient air temperatures were measured by the chamber's shielded sensor placed in the middle of the chamber and at the base of the plants. Temperatures within the chambers were controlled to within 1 C°. All temperature changes were made over a one hour period.

Humidity/Carbon Dioxide/Air Movement

No humidity control was attempted, nor was the humidity of the air stream monitored. No carbon dioxide control was provided. The fan for circulating air within the chamber was set at low; actual air flow rates were not measured.